GENETICS

A PERIODICAL RECORD OF INVESTIGATIONS
BEARING ON HEREDITY AND
VARIATION

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Page 117, next to last line, for "$p=\sqrt{uv}$" read "$p=2\sqrt{uv}$."

Page 121, last column of table 2, line 9, for "$h^2=h^2$" read "$h^2=h_0^2$."

Page 121, last line add, "and use $h^2=\dfrac{4h_0^2(1-p^2)}{h_0^2(1-4p^2)+3}$

Page 125, line 4, for "$=b^2m$" read "$f=b^2m$."

Page 127, table 1, heading, for "$a^2=\frac{1}{2}(1+f)$" read "$a^2=\dfrac{1}{2(1+f)}$"

Page 130, line 7 from bottom, for "a" read "as."

Page 137; line 2, for $\dfrac{\text{"139"}}{519}$ read $\dfrac{\text{"139"}}{512}$

Page 153, next to last line, for "pAa" read "$p'Aa$" and for "$1/2(1-p)aa$" read "$1/2(1-p')aa$."

Page 217, table 5, headings, for "S_uT_u, S_ut_u, s_uT_u, s_ut_u" read "CT_u, Ct_u, cT_u, ct_u."

Page 448, footnote 2, line 1, for "*amblyomyopic*" read "*amblyopic*."

Page 448, footnote 2, line 2, for "*fraction*" read "*refraction*."

Page 491, table 1, column 4, line 5, for "29" read "3."

Page 491, table 1, column 6, line 5, for "23.39" read "2.42."

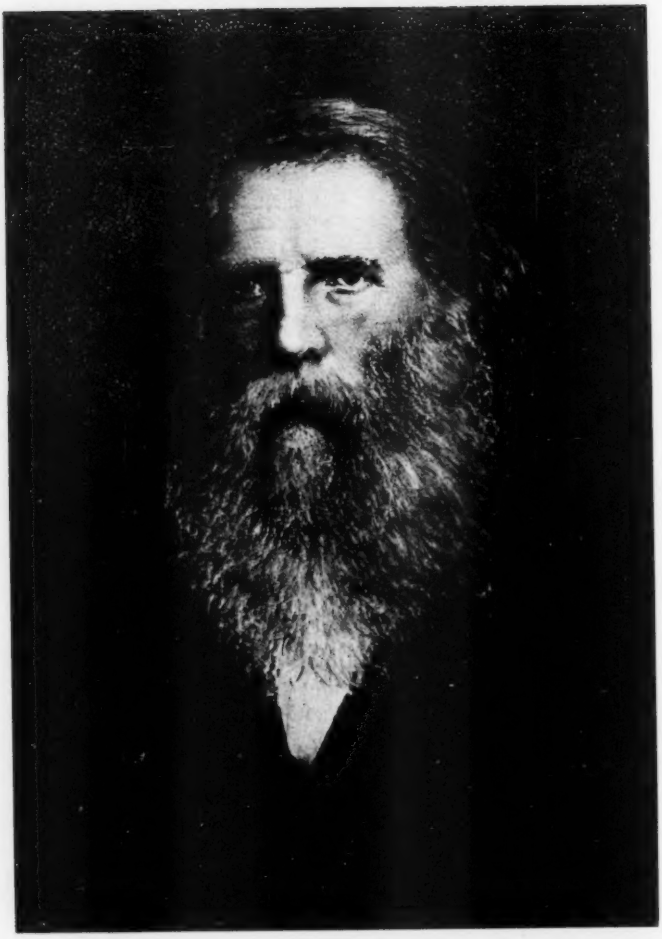
Page 514, line 14, for "$r=.25\sqrt{a+b+d+15c}$" read "$r=.25\sqrt{a+b+d-15c}$."

Page 525, line 8, for volume "41" read volume "46."

Page 525, line 11, for volume "46" read volume "51."

Page 568, diagram of experiment 11, line 2, extreme right-hand, for "(*white*)" read "(*white* ♀)."

Page 569, diagram of experiment 21, line 4, for "$2B'B'r_xr_y$" read "$2B'b'r_xr_y$."



Ch. Darwin

CHARLES NAUDIN

(FRONTISPIECE)

CHARLES NAUDIN, A.B., B.S., Sc.D., Chevalier of the Legion d'honneur, was born at Autun, France, August 14, 1815, and died at Villa Thuret, Antibes, France, March 19, 1899, after a distinguished career as taxonomic botanist, horticulturist, investigator, founder and director of botanical gardens. Orphaned at an early age he was taken in charge by one of his mother's sisters, and on her estate, the Park of St. John, at Autun, he had already acquired at the age of nine and ten the taste for work with plants which so strongly characterized his whole career. His schooling, begun at Autun, was continued successively at Bailleu, Limoux, Montpellier, Autun, Chateau-Chinon and Dijon. He received his A.B. degree at the latter in 1836, and returning to Montpellier took a B.S. degree the following year. He entered a medical school but remained less than a year. He then went to Paris where he functioned for several years as secretary of the Court of Courchamp. This occupation was not particularly agreeable to him, but being thrown wholly on his own resources, he had to earn his daily bread. In 1839 he entered the employ of the Jardin des Plantes as a simple gardener while continuing his studies at night. In 1841 he became a licentiate and received his degree of Doctor of Science in 1842 with a thesis on the "Vegetation of Solanum." In the meantime he wrote articles for the various botanical and horicultural journals and collaborated with AUGUSTE DE SAINT-HILAIRE on a "Revue de la flora du Bresil méridional." In 1843 he began his own study of the Melastomaceae of southern Brazil.

DECAISNE secured NAUDIN'S nomination as Substitute Professor of Zoology at CHAPTAL COLLEGE where DECAISNE himself was Professor of Botany, but NAUDIN had to resign this Professorship owing to an incurable hardness of hearing which soon isolated him from oral intercourse with mankind. Unhappily this deafness was accompanied by a severe facial neuralgia, and although he got partial temporary relief from two operations, he was never free from pain from this time until his death. The severity of the pain more than once interfered with his ardor for his work.

In 1854 DECAISNE took NAUDIN as his assistant and incited him to seek a more scientific basis of species, to study their origin and especially to determine the rôle of hybridity in their production. NAUDIN began at once to collect Cucurbitaceae and to hybridize them. He soon found that they fell into a small number of species, *C. maxima*, *C. pepo*, *C. moschata*, incapable of intercrossing.

In 1860 the Academy of Science of Paris offered a grand prize for the best paper on hybridity in plants particularly in relation to the origin of species, and this prize was awarded to NAUDIN in December, 1862. The memoir entitled "Nouvelle recherches sur l'hybridité dans les végétaux" was published in 1865 in the Nouvelle Archives du Muséum d'Histoire Naturelle 1: 25–176, with 9 plates, mostly colored. The most extensive experiments were with Cucurbitaceae, Papaveraceae and Solanaceae.

This paper, representing eight years of investigation of hybridization phenomena, was published almost simultaneously with MENDEL'S classic paper, and has often been referred to as having barely missed anticipating or at least sharing MENDEL'S discoveries, but NAUDIN'S basic materials and his

conception of the problems to be solved were fundamentally unlike those of MENDEL, and even though some Mendelian phenomena came under observation, they were relatively too meager and insignificant to attract NAUDIN'S special attention. He had no conception of separable unit characters, but only of a single specific "essence" in each species. His formulation of the behavior of two such specific essences brought together in hybrid combination has a remarkable resemblance to MENDEL'S formulation of the behavior of a single pair of unit differences, but the resemblance is purely formal.

NAUDIN found no evidence that new species can originate as a result of hybridization and concluded that hybrids return sooner or later to the original specific types. His views of hybrid behavior were strongly affected, as were DARWIN'S also, by a misconception of the nature of the classic chimaera or "graft-hybrid," *Cytisus Adami*. NAUDIN was of a philosophical turn of mind as many of his discussions of species and related problems show. In a paper published in 1852 he maintained that Nature produces species by the same methods that the practical breeder creates his new varieties of economic plants and animals, thus anticipating by about seven years the presentation of the natural selection hypothesis of DARWIN.

In 1869 NAUDIN left Paris for Collioure on the Mediterranean coast near the junction between France and Spain, in the hope that the warmer climate would act beneficially on his neuralgia. There he founded a botanical garden and experiment station which he directed and developed for nine years. In 1878 he was invited to become director of a similar garden which had been established at Villa Thuret, Antibes, France, and turned over to the state as an adjunct to the Museum of Natural History of Paris. He continued in this position until his death in 1899.

Besides his decoration as Chevalier du Legion d'honneur, already mentioned, he was made a Commander of the Order of the Rose, of Brazil, and Chevalier of the Greek Order of the Savior. A street in his native city of Autun was named for him, and he received in 1897 the Veitch Commemorative Medal in recognition of his services to botany and horticulture.

The portrait here reproduced was published shortly after NAUDIN'S death in Bulletin 12 of the Société d'histoire naturelle d'Autun, in connection with an appreciative biographical sketch by B. RENAULT. The data for the present sketch are largely derived from a biography by ED. BORNET published in the Comptes Rendus des Séances de l'Acad. Sci. Paris, for March 27, 1899. The funds for the reproduction of this portrait were generously provided by Doctor JOHN C. PHILLIPS, well known to geneticists for his surgical work in connection with transplantation of ovaries, and for his extensive hybridization experiments with ducks and pheasants.

A CASE OF MENDELIAN INHERITANCE COMPLICATED BY HETEROGAMETISM AND MUTATION IN *OENOTHERA PRATINCOLA*[1]

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Received June 21, 1920

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INTRODUCTION

In the study of heredity in the genus Oenothera simple Mendelian results are very rarely obtained. It is generally conceded that the unusual results are due to the production, by a single morphologically uniform strain, of gametes of more than one type. The explanations have been various. The mutation hypothesis of DE VRIES is of course well known. It has not been generally accepted, however, as originally proposed. MORGAN (1918) and MULLER (1918) have suggested point mutation, followed by crossing over, an explanation suggested by their work on Drosophila. MULLER has worked out experimentally a balanced lethal stock of Drosophila in which certain seemingly aberrant phenomena of the Oenotheras find a parallel. To what extent the parallel affords an explanation we can not judge until the genetic analysis of the Oenotheras has been carried further.

[1] Papers from the Department of Botany of the UNIVERSITY OF MICHIGAN, No. 181.

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The present paper is a contribution to the genetic analysis of *Oenothera pratincola*. It deals exhaustively with the first case in which simple Mendelian inheritance has been recognized and conclusively demonstrated when complicated by phenomena peculiar to the Oenotheras.

The strains of *Oenothera pratincola* used in this investigation were those of which the history has already been published (BARTLETT 1915 a, b; COBB and BARTLETT 1919). Although morphologically alike, one of them, designated as strain E, is genetically different from the other seven, of which strain C, the strain used in the experiments recorded in this paper, is a typical example.

Strain C produces in every generation a small number of mutations of several kinds (BARTLETT 1915 a). Some of these kinds appear also in strain E, but much more conspicuous in strain E are numerous mutations, of a strikingly distinct series, which do not occur in the other strains. These mutations occur in such numbers as to merit the term mass mutation (BARTLETT 1915 b) as a designation of the phenomenon. The series consists of four distinct types, all alike in having narrow, strongly revolute leaves, and in producing nothing but revolute-leaved plants in their progenies. Of these revolute-leaved mutations, mut. *formosa* (BARTLETT 1915 b), the strongest and most fertile of the series, was crossed with f. *typica* of strain E, and with strain C.

In a former paper (COBB and BARTLETT 1919) it has been stated that in reciprocal crosses between mut. *formosa* and f. *typica* E, from which mut. *formosa* arises, inheritance is matroclinic. Strain C pollinated by mut. *formosa* gives a matroclinic progeny; but the reciprocal cross, mut. *formosa* pollinated by strain C, gives in the F_1 generation only f. *typica*, in the F_2 generation a Mendelian segregation of 3 f. *typica*: 1 mut. *formosa*.

HYPOTHESIS OF HETEROGAMETISM

The hypothesis of heterogametism offered (COBB and BARTLETT 1919) in explanation of these phenomena, assumes that two types of gametes occur in *Oenothera pratincola*, α gametes (usually female) and β gametes (usually male), the α gametes carrying some factors not represented in the β gametes. Each zygote is formed by the union of an α and a β gamete, and so gets (except in rare cases of metacliny) the α determiners of its pistillate parent and the β determiners of its staminate parent. It, in turn, produces α (female) and β (male) gametes. In the case of a cross, the zygote is quite unaffected by the nature of the α of its staminate parent and the β of its pistillate parent.

Besides its characteristic α or β part, each gamete carries a group of factors common to both α and β gametes. The characteristic α and β portions of the gametes may consist of a single chromosome or of a group of chromosomes, but probably the latter, for very few characters have been found which are not connected with the α or β portions of the gametes. At reduction, α and β behave as units; that is, there is no interchange of factors or chromosomes between the characteristic α and β portions, each passing into the gametes (the α into the female, the β into the male) just as it entered the zygote from the parent. There is, however, the usual free segregation among the remainder of the chromosomes, each member of the homologous pairs accompanying with equal frequency the α and the β portions. Thus factors entering a zygote in the characteristic α or β chromosome (or chromosomes) occur in the α or β gametes, respectively, which it produces; but those factors which entered the zygote in the remaining, freely segregating group of chromosomes, occur as frequently in the α as in the β gametes produced. Characters whose factors belong to the α or to the β portion are inherited matroclinically or patroclinically, respectively; those whose factors belong to homologous and freely segregating chromosomes common to both α and β gametes are inherited in a Mendelian manner.

Mut. *formosa* arose from f. *typica* E by modification of a factor for flatness in the α portion of the α gamete, that is, by change of a factor which has no counterpart in the β portion of the β gamete. Change being in the α (female) gamete only, inheritance in crosses between mut. *formosa* and f. *typica* E is therefore matroclinic. If mut. *formosa* is used as the pistillate parent the α gamete received by the progeny is the mutated α of mut. *formosa* (designated hereafter as α'), and the progeny is therefore mut. *formosa;* if f. *typica* is used as the pistillate parent the α gamete received by the progeny is the normal α gamete of *Oenothera pratincola*, and the progeny is f. *typica*.

Strain C differs from strain E in having, in addition to the factor for flatness in the α portion of the α gamete, a freely segregating (Mendelian) factor for flatness (*F*) present in both α and β gametes, of which the recessive allelomorph (*f*) is carried by strain E. Thus the constitution of strain C is $\alpha\beta FF$, and the gametes which it produces are αF (female) and βF (male). The constitution of strain E is $\alpha\beta ff$, and the gametes which it produces are αf (female) and βf (male). The constitution of mut. *formosa* is $\alpha'\beta ff$, and the gametes which it produces are $\alpha' f$ (female) and βf (male). Therefore strain C ($\alpha\beta FF$) pollinated by mut. *formosa* ($\alpha'\beta ff$) gives a flat-leaved progeny ($\alpha\beta Ff$) which breeds true, for the α gamete

concerned in the cross is normal; but mut. *formosa* ($\alpha'\beta ff$) pollinated by strain C ($\alpha\beta FF$) gives a flat-leaved progeny ($\alpha'\beta Ff$) (flat-leaved, notwithstanding the mutated condition of α', because of the presence of one Mendelian factor for flatness, inherited from the pistillate parent) which shows in the next generation a Mendelian segregation of flat-leaved plants ($\alpha'\beta FF$ and $\alpha'\beta Ff$) and revolute-leaved plants ($\alpha'\beta ff$). The α' gamete concerned in the cross has lost the factor for flatness, and so those F_2 individuals that are recessive for the Mendelian factors for flatness show the revoluteness determined by α'. This new synthetic f. *typica* ($\alpha'\beta FF$ or $\alpha'\beta Ff$), differing in genetic composition from both f. *typica* C and f. *typica* E, carrying the factor for revoluteness masked by at least one of the Mendelian pair of factors for flatness, will be called f. *typica* M (homozygous or heterozygous, as the case may be).

The hypothesis of the genetic constitution of the plants, and the results of crossing, may be stated in brief as follows:

Strain C,	$\alpha\beta FF$, flat, and, with respect to this character, immutable.
Strain E,	$\alpha\beta ff$, flat, mutable.
Mut. *formosa*,	$\alpha'\beta ff$, revolute-leaved.
Strain E × *formosa*,	$\alpha\beta ff$, flat, mutable.
Formosa × strain E,	$\alpha'\beta ff$ revolute, breeding true with respect to this character.
Strain C × *formosa*,	$\alpha\beta Ff$ flat, segregating with respect to mutability.
(Strain C × *formosa*) F_2	1 $\alpha\beta FF$ flat, immutable, breeding true. 2 $\alpha\beta Ff$ flat, continuing the segregation of the F_1 generation. 1 $\alpha\beta ff$ flat, mutable, otherwise breeding true.
Formosa × strain C,	$\alpha'\beta Ff$ flat, segregating with respect to revoluteness.
(*Formosa* × strain C) F_2	1 $\alpha'\beta FF$ flat, non-segregating. 2 $\alpha'\beta Ff$ flat, continuing the segregation of the F_1 generation. 1 $\alpha'\beta ff$ revolute, breeding true.

EQUIVALENCE, WITHIN STRAIN C, OF POLLEN OF OENOTHERA PRATINCOLA F. TYPICA AND MUT. LATIFOLIA

The former paper (COBB and BARTLETT 1919) gave data of the F_1 and F_2 generations of the cross mut. *formosa* E × mut. *latifolia* C. At the time the original crosses between mut. *formosa* and strain C were made,

the cross mut. *formosa* × f. *typica* C was unsuccessful. But the pollen of mut. *latifolia* had been shown to be equivalent to the pollen of the f. *typica* from which it arises (the mutation to *latifolia* being concerned with the α gamete, the β gamete remaining as in f. *typica*), and therefore, in order to have a more complete series of crosses to work upon, the cross mut. *formosa* × mut. *latifolia* from strain C was used in place of the missing cross, mut. *formosa* × f. *typica* C. The substitution has been justified by later work, recorded in tables 5 and 6 of the present paper, which give analyses of the F_1 and F_2 generations of the cross mut. *formosa* × f. *typica* C. This cross was successfully made three years after the original crosses upon which much of the work recorded here is based.

The F_1 generation (see table 5) consisted of 100 plants from six different crosses, all of them flat-leaved. The F_2 generation (see table 6) consisted of 3274 plants, 2399 flat-leaved and 875 revolute-leaved; that is, a ratio of 2.74:1, in sufficiently good accord with the 3:1 of the Mendelian monohybrid ratio. The cross mut. *formosa* × mut. *latifolia* C, as recorded in the previous paper, gave in the F_1 generation 209 plants, all of them flat-leaved, and in the F_2 generation from normal f. *typica* plants of the F_1 generation, 6392 plants, 4759 flat-leaved and 1633 revolute-leaved; that is, a ratio of 2.91:1. This shows that the results in the F_2 generation are the same whether mut. *formosa* is pollinated by f. *typica* C or by mut. *latifolia* C; and this, in connection with the previous evidence (COBB and BARTLETT 1919) of the equivalence of the pollen from the two sources, gives ample justification for the substitution of f. *typica* M descended from mut. *latifolia* instead of the identical form descended from f. *typica* C.

THE F_3 AND F_4 GENERATIONS OF THE CROSS MUT. FORMOSA FROM STRAIN E × MUT. LATIFOLIA FROM STRAIN C

The F_3 and F_4 generations of the cross mut. *formosa* × mut. *latifolia* C show a continuance of the Mendelian behavior of the F_2 generation (COBB and BARTLETT 1919). Self-pollination of normal f. *typica* plants of the F_2 generation gave in the F_3 generation (see table 2) 22 progenies consisting entirely of flat-leaved plants, showing the presence of homozygous dominants ($\alpha'\beta FF$) in the F_2 generation, and 41 progenies in which there were both flat-leaved and revolute-leaved plants, showing the presence of heterozygous dominants ($\alpha'\beta Ff$) in the F_2 generation. The ratio 22 uniform cultures to 41 segregating cultures very closely approximates the expected ratio of 1 homozygous dominant to 2 heterozygous dominants in the F_2 generation. In the segregating progenies of the F_3 generation

the ratio of flat-leaved to revolute-leaved plants is 3.08:1, in very close agreement with the expected 3:1 of the Mendelian monohybrid segregation.

All progenies of fewer than 20 plants were omitted from table 2 as being unreliable. A very small culture of flat-leaved plants might, had it been larger, have included some revolute-leaved plants, and thus a heterozygous dominant of the F_2 generation might be recorded as homozygous. If these cultures were included in the table, the ratio of non-segregating to segregating progenies would become 33:56 instead of 22:41, and the ratio of flat-leaved to revolute-leaved plants in the segregating progenies would become 2.94:1 instead of 3.08:1.

Self-pollination of 16 plants of f. *typica* M ($\alpha'\beta FF$) belonging to the non-segregating cultures of the F_3 generation gave in the F_4 generation (see table 3) 1114 plants, all of them flat-leaved. From these plants an F_5 generation has been grown, consisting of 695 plants belonging to 7 progenies, no progeny consisting of fewer than 29 plants. All were flat-leaved. Self-pollination of 3 plants chosen at random among the f. *typica* plants of the segregating cultures of the F_3 generation gave in the F_4 generation (see table 4) 2 segregating progenies and 1 non-segregating, showing a continuance of the Mendelian splitting to the fourth filial generation. It seems unnecessary to carry the line further.

The behavior of the recessives, mut. *formosa* ($\alpha'\beta ff$), of the F_2 generation of the cross mut. *formosa* × mut. *latifolia* C. was also in accord with expectation. The F_3 generation consisted of 69 plants belonging to progenies of 4 mut. *formosa* plants of the F_2 generation. All were revolute-leaved, and the 62 grown to maturity all proved to be mut. *formosa*. Also, 2388 plants belonging to the F_3 progenies from mut. *formosa* plants of the F_2 generation, of the cross mut. *formosa* × CD hyb. *viscida* were all revolute-leaved. Hyb. *viscida* is the form resulting from the cross *Oenothera pratincola* f. *typica* C × *Oenothera numismatica* (BARTLETT 1915 a). It is like f. *typica* C in all respects, except that, in addition to the pubescence normally occurring on the flowers of *Oenothera pratincola*, it has the viscid pubescence of *Oenothera numismatica*.

THE F_1 AND F_2 GENERATIONS OF THE CROSS F. TYPICA, STRAIN C × MUT. FORMOSA, STRAIN E

The Mendelian behavior following the cross mut. *formosa* × strain C has been demonstrated at length. The reciprocal cross, f. *typica* C × mut. *formosa* ($\alpha\beta FF \times \alpha'\beta ff$), is just as Mendelian in its segregation of the free factors for flatness, but the Mendelian segregation of factors finds no

chance to express itself in the zygote because of the ever-present α factor for flatness inherited from the pistillate parent. The only way for a revolute-leaved plant to occur in the F_2 or following generations of the cross is by an independent mutation from α to α' in the presence of the recessive condition of the Mendelian factors for flatness. Only one-fourth of the plants of the F_2 generation, those with the constitution $\alpha\beta ff$, are capable of becoming revolute-leaved by mutation. Apparently there is nothing to hinder mutation from α to α' in strain C. But in pure strain C the change would not be indicated by outward sign, for the strain is homozygous for the Mendelian factors for flatness. That this change does sometimes occur is shown by the few revolute-leaved plants which occur in the F_2 generation of the cross f. *typica* C $\times$ mut. *formosa* (see table 8, and COBB and BARTLETT 1919, table 6). In table 8 there are 26 revolute-leaved plants in a total of 1654, or 16 per 1000. If the mutation to α' should take place in a plant of the F_1 generation ($\alpha\beta Ff$), a 3:1 ratio would occur in the F_2 generation. In the hope that this may sometime happen in the experiment garden, the cross f. *typica* C $\times$ mut. *formosa* has been repeated many times, and F_1 and F_2 progenies are being grown.

THE F_1 AND F_2 GENERATIONS OF THE CROSS MUT. FORMOSA STRAIN E $\times$ F. TYPICA STRAIN E

In the cross mut. *formosa* $\times$ f. *typica* E ($\alpha'\beta ff \times \alpha\beta ff$) the mechanism for Mendelian inheritance operates just as certainly as in the corresponding cross with f. *typica* C, but the two parents happen to be alike in the Mendelian factors under consideration, both being pure recessives, so the only type of inheritance which manifests itself is matrocliny, depending on the difference in factorial composition of the characteristic portions of the α and β gametes. This cross has been repeated successfully nine times, giving 305 plants in the F_1 generation (see table 9) and 628 plants, from four plants of the F_1 generation, in the F_2 generation (see table 10). All of the plants of both generations were revolute-leaved. The inheritance here is matroclinic, in contrast with the Mendelian inheritance in the corresponding cross with strain C.

The reciprocal cross, f. *typica* E $\times$ mut. *formosa* ($\alpha\beta ff \times \alpha'\beta ff$), has not been successfully repeated since the publication (COBB and BARTLETT 1919) of the fact that this cross is also matroclinic, the number of revolute-leaved plants occurring in the progeny being no greater than might be expected from self-pollination of f. *typica* plants of strain E, the strain which regularly produces some revolute-leaved plants in every generation.

THE F_1 AND F_2 GENERATIONS OF VARIOUS CROSSES BETWEEN F. TYPICA M (THE NEW, MENDELIAN STRAIN) AND F. TYPICA OF STRAIN C, F. TYPICA OF STRAIN E, AND MUT. FORMOSA

The data recorded in this paper concerning the F_1 and F_2 generations of crosses of eighteen different kinds between f. *typica* M (the new Mendelian strain from the cross mut. *formosa* × strain C) as one parent, and f. *typica* C, f. *typica* E, or mut. *formosa*, as the other parent, confirm the hypotheses of non-equivalent gametes and the presence of a pair of independent Mendelian factors in *Oenothera pratincola*.

All f. *typica* M plants used in the crosses were self-pollinated to determine whether they were homozygous or heterozygous.

All of the flat-leaved types other than f. *typica* which occurred in the progenies of crosses are mutations regularly thrown by f. *typica* C, and some of them by f. *typica* E also. All of the revolute-leaved types which occurred, are regularly thrown by f. *typica* E and by mut. *formosa*.

The cross mut. *formosa* × f. *typica* M (homozygous) ($\alpha'\beta ff \times \alpha'\beta FF$) gave in the F_1 generation (see table 11) only flat-leaved plants ($\alpha'\beta Ff$), and in the F_2 generation (see table 12) a segregation of 3 flat-leaved plants ($\alpha'\beta FF$ and $\alpha'\beta Ff$) to 1 revolute-leaved plant ($\alpha'\beta ff$).

The reciprocal cross, f. *typica* M (homozygous) × mut. *formosa* ($\alpha'\beta FF \times \alpha'\beta ff$), gave the same results (see tables 13 and 14).

The cross mut. *formosa* × f. *typica* M (heterozygous) ($\alpha'\beta ff \times \alpha'\beta Ff$) gave in the F_1 generation (see table 15) progenies consisting of flat-leaved plants ($\alpha'\beta Ff$) and revolute-leaved plants ($\alpha'\beta ff$) in approximately equal numbers, and in the F_2 generation from flat-leaved plants (see table 16) a segregation of 3 flat-leaved plants ($\alpha'\beta FF$ and $\alpha'\beta Ff$) to 1 revolute-leaved plant ($\alpha'\beta ff$).

The reciprocal cross, f. *typica* M (heterozygous) × mut. *formosa* ($\alpha'\beta Ff \times \alpha'\beta ff$) gave the same results (see tables 17 and 18).

The cross f. *typica* E × f. *typica* M (homozygous) ($\alpha\beta ff \times \alpha'\beta FF$) gave in both the F_1 and the F_2 generations (see tables 19 and 20) only flat-leaved plants. It is known that the α of strain E frequently mutates to α', and a few revolute-leaved plants would therefore be expected in the F_2 progenies, by a combination of α' and the recessive Mendelian factors. One-fourth of the plants of the F_2 generation, those with the constitution $\alpha\beta ff$, would be expected to become revolute-leaved by mutation with the frequency of mutation in pure strain E. But this did not occur. The only explanation that can be suggested is that because the germination percentage was much higher than was expected, the seedlings were very much crowded in

the seed-pans, and possibly revolute-leaved plants, which do not hold their own in a dense stand, died before the seedlings were counted off. This, however, does not seem likely, and the matter will be further investigated.

The reciprocal cross, f. *typica* M (homozygous) × f. *typica* E ($\alpha'\beta FF \times \alpha\beta ff$), gave in the F_1 generation (see table 21) only flat-leaved plants ($\alpha'\beta Ff$) and in the F_2 generation (see table 22) a segregation of 3 flat-leaved plants ($\alpha'\beta FF$ and $\alpha'\beta Ff$) to 1 revolute-leaved plant ($\alpha'\beta ff$).

The cross f. *typica* M (heterozygous) × f. *typica* E ($\alpha'\beta Ff \times \alpha\beta ff$) gave in the F_1 generation (see table 23) flat-leaved plants ($\alpha'\beta Ff$) and revolute-leaved plants ($\alpha'\beta ff$) in about equal numbers, and in the F_2 generation from flat-leaved plants (see table 24) a segregation of 3 flat-leaved plants ($\alpha'\beta FF$ and $\alpha'\beta Ff$) to 1 revolute-leaved plant ($\alpha'\beta ff$).

The reciprocal cross is missing from the series.

The cross f. *typica* M (homozygous) × f. *typica* C ($\alpha'\beta FF \times \alpha\beta FF$) gave in both the F_1 and F_2 generations (see tables 25 and 26) only flat-leaved plants ($\alpha'\beta FF$ in both generations).

The reciprocal cross is missing from the series.

The cross f. *typica* M (heterozygous) × f. *typica* C ($\alpha'\beta Ff \times \alpha\beta FF$) gave in the F_1 generation (see table 27) only flat-leaved plants ($\alpha'\beta FF$ and $\alpha'\beta Ff$) and in the F_2 generation (see table 28) 11 progenies consisting entirely of flat-leaved plants ($\alpha'\beta FF$) and 7 progenies showing a segregation of 3 flat-leaved plants ($\alpha'\beta FF$ and $\alpha'\beta Ff$) to 1 revolute-leaved plant ($\alpha'\beta ff$). The ratio 11:7 does not approach as closely as would be expected the ratio of one dominant factor to one recessive factor in the gametes of the heterozygous pistillate parent of the cross. In this table there seems to be a shortage both of segregating progenies and of revolute-leaved plants in the segregating progenies, indicating that the pistillate parent and its progeny produce either fewer or weaker gametes bearing the recessive factor.

The reciprocal cross is missing from the series.

A summary of tables 5 to 28, inclusive, is given as table 29.

VARIOUS PEDIGREES OF PLANTS USED IN CROSSES

A record of the parentage of all of the plants used in this work is given as table 1. All plants not otherwise designated were f. *typica*.

It may be noticed that, though different strains of *Oenothera pratincola* behave differently as to the mutations that they throw when self-pollinated, and in the way that they behave in crosses, all f. *typica* plants within a strain, no matter how complicated, by crossing or mutation, their pedi-

grees may be, act in the same way. For instance, an f. *typica* from mut. *grisella* from f. *typica* C behaves exactly as f. *typica* C with no mutations in its direct ancestry, at least during the period in which the strain has been carried in the garden.

It may also be noted that all plants of mut. *formosa* appear the same and behave the same genetically regardless of extraction. Those used in crosses were of five different types of extraction: (1) directly from f. *typica* E, by self-pollination; (2) from f. *typica* E, first by mutation to *angustifolia*, then to mut. *nitidissima* and finally to mut. *formosa*, all by self-pollination; (3) from the cross mut. *formosa* × f. *typica* E, by matroclinic inheritance; (4) from the cross mut. *formosa* × strain C, by segregation; (5) from crosses with both strain C and strain E, by segregation and matroclinic inheritance, e.g., ((mut. *formosa* × mut. *latifolia* C)—mut. *formosa* × f. *typica* E)—mut. *formosa*.

In many thousand offspring, mut. *formosa* has produced nothing but revolute-leaved plants.

DISCUSSION

It may seem to those who are used to working with organisms in which clear Mendelian inheritance is the usual thing, that this case in *Oenothera pratincola* has been worked out with unnecessary elaboration. But several considerations should be borne in mind: first, that evident Mendelian inheritance is so rare in Oenothera that only two indisputable cases have been recorded, that of mut. *brevistylis* (DE VRIES 1901, p. 223; 1903, pp. 151–179, 429) and that of the dwarf mutation from mut. *gigas* (DE VRIES 1915 b) and that all instances deserve therefore to be thoroughly examined; second, that in this case the Mendelian inheritance is apparently modified by inheritance of another kind, working simultaneously with and independently of the Mendelian inheritance; and third, that the hypothesis of heterogametism put forth to explain this other type of inheritance needs further testing.

If the explanations offered here are correct, we have, in addition to Mendelian inheritance masked by heterogametism, mutation masked by Mendelian factors. That the α of strain C can undergo mutation to α' is shown by the presence of a few revolute-leaved plants in the F_2 generation of the cross f. *typica* C × mut. *formosa*. These plants derive their α from strain C, but have the dominant Mendelian factors which are present in strain C replaced by their recessive allelomorphs (see table 8). There seems no reason to doubt that this mutation in α occurs just as frequently in the presence of the Mendelian factors for flatness (i.e., in pure strain C)

as in their absence. If such is the case, Mendelian factors hide the mutation until a suitable cross occurs to remove the factors. This may have some bearing on the question whether crossing induces mutation; it may be that crossing merely makes possible an external expression, by removing concealing Mendelian factors, of changes which occurred long since in the germ-plasm and have been passed on from generation to generation giving no visible sign of their presence. In the same way a single mutation, the loss of one concealing factor, in a single chromosome, might bring to light a whole series of new forms. (The several revolute-leaved types that have occurred in the experiment garden can all be permanently concealed by the single pair of Mendelian factors for flatness.) This may explain in part the apparent periodicity of mutability. Perhaps the organism does not have increased tendency to change, but hoards actual changes until chance brings them to light, "gruppenweise," by the removal of inhibiting factors through a mutation.

Though the condition of the Mendelian factors in *Oenothera pratincola* strains other than strains C and E has not been investigated, it seems probable, since they have given no revolute-leaved plants, that the other six strains are homozygous with regard to the factor for flatness. If strain E is the only one of the eight strains carrying the recessive factors, it might seem likely that it arose from one of the other strains by loss of a dominant factor, and consequent Mendelian segregation, rather than that the reverse change took place, were it not for the fact that strain E has produced in the experiment garden a mutation (mut. *nitidissima*) which, as shown by its behavior in crosses with mut. *formosa*, is a homozygous dominant in regard to the Mendelian factors for flatness. Whether both dominant factors were present in the original plant of mut. *nitidissima* and its F_1 generation is a question which cannot be answered, but it is clear that they are now present in the strain as it is carried on in the garden.

That a pure dominant strain might arise from a pure recessive strain, or the reverse, leaving no heterozygous plants to tell the tale, seems possible, for the heterozygotes, as they appear in the experiment garden, tend to have poor and irregular leaf development as young rosettes, and might easily be eliminated by natural selection. The modification of a factor for flatness in a single chromosome of a homozygous dominant, or the reverse modification in a homozygous recessive, would then be the only change in the germ-plasm necessary to produce one homozygous strain from the other.

Some explanation should be made of the unusually low germination percentages occurring in the cultures recorded in this investigation. As the

character flatness vs. revoluteness is one which is evident in even very young seedlings, many sowings were made merely for the sake of recording the nature of the seedlings, and the seedlings were then discarded. In order to give all possible space and attention to the cultures intended for the summer garden at the time which is most favorable for planting, the sowings for seedling counts were made early and got out of the way. This meant that the seeds did not have as long a rest period as they apparently need before germination. Had they been planted a month or two later (in February and March instead of December and January) the percentages of germination would have been very much higher.

In problems connected with comparative fertility and sterility it is of course quite necessary to know that all viable seeds are forced to germinate. The method worked out by DE VRIES (1915 a) and applied by DAVIS (1915) for forcing germination to completion, is especially suited to such problems. It will also throw light on the types that may be lost through selective mortality and selective germination rate when less thorough methods are used. This information is most valuable. But that the low germination percentage has no significant effect on the results of the experiments recorded here is shown by table 30. Here the ratios of flat-leaved to revolute-leaved plants are assembled from all of those cultures in which the expected ratio is 3:1, and arranged according to the germination percentage. It will be seen that three-fourths of the cultures have a germination percentage under 25 percent. But it may also be seen that the average of the ratios of cultures in which the germination is from 50 to 81 percent is no nearer the expected 3:1 ratio than are the averages from cultures with poorer germination. Even when less than 5 percent of the seeds germinated, the average is as close to the theoretical ratio as is that of any one of the five cultures with a germination over 50 percent, or as the average of these five cultures.

That selective germination, in connection with the types with which this problem is concerned, occurs to any significant extent seems impossible. The only evidence of such selection is a slight excess of revolute-leaved individuals, especially noticeable when the germination is poorer. There are four tables which show in the total an excess of flat-leaved plants, ten which show an excess of revolute-leaved plants. In work with this species it has been noticed that when the percentage of germination is very low the percentage of mutations is very high (BARTLETT 1915 a). General observations lead to the conclusion that poor germination tends to bring the unusual types into prominence rather than to conceal them.

This paper records the case of a single unit character of the zygote, revoluteness, determined by a complicated set of phenomena: an allelomorphic pair of factors (*F* and *f*), the dominance and recessiveness of which produce no effect on the zygote except when the particular mutational change from α to α' has taken place; a mutation (α to α') occurring repeatedly, but concealed, as long as self-pollination continues, by the Mendelian factors *FF*, and Mendelian segregation concealed by matroclinic inheritance dependent on heterogametism (α and β gametes). It is hoped that the case may help to throw light upon the seemingly peculiar behavior of the Oenotheras.

SUMMARY

1. The male and female gametes of *Oenothera pratincola* are not alike. Each zygote is formed by the union of an α (female) gamete and a β (male) gamete (except in rare cases which it is needless to mention here) and has the constitution $\alpha\beta$. It, in turn, produces α (female) and β (male) gametes.

2. The α (female) gametes may undergo such mutation that, unless certain factors for flatness are present, the resulting plants are revolute-leaved. Such mutated gametes are designated α'.

3. The β (male) gametes have no such possibility of producing revolute-leaved plants.

4. Strain C carries in both male and female gametes, but not in the characteristic α and β portions of the gametes, a freely segregating factor for flatness (*F*), in the presence of which revoluteness can not occur, even though the mutation to α' has occurred. The constitution of f. *typica* strain C is $\alpha\beta FF$.

5. Strain E does not carry in either male or female gametes the independent factor for flatness which occurs in strain C, but its allelomorph (*f*). The constitution of f. *typica* strain E is $\alpha\beta ff$.

6. Mut. *formosa*, a revolute-leaved mutation thrown by strain E, differs from f. *typica* strain E in that it contains a mutated α (α'). The constitution of mut. *formosa* is $\alpha'\beta ff$.

7. There are two types of inheritance going on simultaneously and independently in *Oenothera pratincola*, matroclinic inheritance, connected with certain constant differences in factorial composition between male and female gametes, and Mendelian inheritance, connected with an independent segregation of factors carried by both gametes.

8. The cross mut. *formosa* $\times$ strain C ($\alpha'\beta ff \times \alpha\beta FF$) produces only flat-leaved plants in the F_1 generation; in the F_2 generation there occurs a Mendelian segregation in the ratio of 3 flat-leaved plants to 1 revolute

leaved plant. This segregation has been followed to the F_4 generation. The f. *typica* plants descended from this cross have the constitution $\alpha'\beta FF$ or $\alpha'\beta Ff$, and are called f. *typica* M (homozygous) and f. *typica* M (heterozygous), respectively.

9. The reciprocal cross, strain C $\times$ mut. *formosa* ($\alpha\beta FF \times \alpha'\beta ff$) also gives only flat-leaved plants in the F_1 generation; but in the F_2 generation there is no Mendelian segregation, though there occurs by mutation a small percentage (1.6 percent) of revolute-leaved plants. In this cross the inheritance appears to be matroclinic.

10. In reciprocal crosses between mut. *formosa* ($\alpha'\beta ff$) and f. *typica* E ($\alpha\beta ff$) the inheritance is purely matroclinic, as the two parents are alike in regard to the Mendelian factors for flatness.

11. The results, recorded in the tables of this paper, of various crosses between f. *typica* M and f. *typica* C, f. *typica* E and mut. *formosa* are all such as to favor the hypotheses of heterogametism and the presence of a pair of Mendelian factors for flatness in *Oenothera pratincola*. All the results obtained could be correctly predicted on the assumption that:

f. *typica* C $= \alpha\beta FF$
f. *typica* E $= \alpha\beta ff$
mut. *formosa* $= \alpha'\beta ff$

12. The α of strain C may become mutated to α', but in pure strain C this change can find no expression, because of the Mendelian factors for flatness for which this strain is homozygous. That the change does sometimes occur here, as in strain E, is shown by the occurrence of a few revolute-leaved plants in the otherwise uniformly flat-leaved F_2 generation of the cross f. *typica* C $\times$ mut. *formosa*, plants in which the α portion of the constitution came from strain C and in which the Mendelian factors for flatness are replaced by their recessive allelomorphs from strain E.

13. The difference, with regard to Mendelian factors, between strains C and E is paralleled by the difference, with regard to the same factors, between mut. *nitidissima*, a type which has arisen in the experiment garden, and strain E from which it arose. Strain E is recessive; mut. *nitidissima* is a homozygous dominant. Evidently a homozygous dominant strain can arise from a homozygous recessive strain; the reverse process has not as yet been known to take place in the garden.

14. It is concluded that mutation may be masked by Mendelian factors, and that the apparent induction of mutation by hybridization may be merely the first appearance of changes which occurred in the past and

were carried on unseen until their appearance in the zygote was made possible by the removal, through hybridization, of inhibiting Mendelian factors.

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APPENDIX—TABLES

Explanations applying to all of the tables

In table 1, all plants not otherwise designated were f. *typica*.

F. *typica* M is the synthetic, Mendelian strain of *Oenothera pratincola* which arises from the cross mut. *formosa* × f. *typica* C (or other form with equivalent pollen).

The numbers in columns headed "Key number" refer to corresponding numbers in table 1. The numbers in columns headed "Parent plant" are the numbers of the individual plants in the progenies resulting from the crosses or self-pollinations recorded in table 1.

* indicates that the seeds sown were from a single capsule.

† indicates that seeds from two or more capsules were sown together.

All of the flat-leaved types mentioned in analyses of cultures are regularly thrown by self-pollinated f. *typica* C, and some of them also by f. *typica* E. All of the revolute-leaved types mentioned are regularly thrown by f. *typica* E and by mut. *formosa*.

Types other than f. *typica*, mut. *latifolia*, and mut. *formosa* mentioned in the following tables are:

Mut. *albicans* (BARTLETT 1915 b, page 449).

Mut. *angustifolia* (BARTLETT 1915 b, page 438).

Mut. *dimorpha*, an undescribed mutation.

Mut. *ericacea*, an undescribed mutation.

Mut. *fallax*, an undescribed mutation, as a seedling very much like mut. *nummularia*, and thrown by the same strains.

Mut. *gigas* (BARTLETT 1915 b, page 443).
Mut. *grisea*, an undescribed mutation.
Mut. *grisella*, an undescribed mutation.
Mut. *nitidissima* (BARTLETT 1915 b, page 440, table IV).
Mut. *nummularia*, a mutation commonly thrown by strain C but never by pure strain E. (BARTLETT 1915 a, page 97; COBB and BARTLETT 1919.)
Mut. *revoluta* (BARTLETT 1915 b, page 450).
Mut. *setacea* (BARTLETT 1915 b, page 450).
Mut. *sub-latifolia*, an undescribed mutation.
Hyb. *viscida*, a hybrid of *Oenothera pratincola* × *Oenothera numismatica* (BARTLETT 1915 a, page 86). This form is like *Oe. pratincola* f. *typica* with the addition of the viscid pubescence of *Oe. numismatica*.

TABLE 1

Record of the parentage of all of the progenies recorded in the following tables with key numbers. All plants not otherwise designated are f. typica

1[1]	E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia*	4
2	E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia*	190
3	E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia*	162
4	E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia*	162 – 164 *formosa* × C – 52 – 6 *grisella*[2] – 31 *grisella* – 73 – 3 (= 3 No. 164 *formosa* × f. *typica* C)
5	E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia*	162 – 153 *formosa* × C – 52 – 6 *grisella* – 31 *grisella* – 73 – 3 (= 3 No. 153 *formosa* × f. *typica* C)
6	E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia*	162 – 30 *formosa* × C – 52 – 6 *grisella* – 31 *grisella* – 73 – 3 (= 3 No. 30 *formosa* × f. *typica* C)

[1] These numbers are designated "key numbers" in subsequent tables.
[2] An undescribed mutation.

TABLE 1 (continued)

7 E – 5 – 199 *formosa* – 28 *formosa* ×
C – 22 – 13 *latifolia* – 87 *latifolia* } 162 – 138 *formosa* ×
C – 52 – 6 *grisella* – 31 *grisella* – 73 – 3
(= 3 No. 138 *formosa* × f. *typica* C)

8 E – 5 – 199 *formosa* – 58 *formosa* – 15 *formosa* ×
C – 52 – 6 *grisella* – 25 – 1 – 41

9 E – 5 – 199 *formosa* – 28 *formosa* ×
C – 22 – 13 *latifolia* – 87 *latifolia* } 162 – 164 *formosa* ×
E – 43 – 89 – 5 – 19 } 2 *formosa* ×
C – 22 – 7 – 40 – 5 – 9 – 2
(= 23 No. 2 *formosa* × f. *typica* C)

10 C – 52 – 6 *grisella* – 25 – 1 – 43 – 2 ×
E – 5 – 199 *formosa* – 58 *formosa* – 15 *formosa* } 63 *formosa*
×
E – 43 – 89 – 5 – 1
(= f. *typica* C × 25 No. 63 *formosa*)

11 C – 52 – 6 *grisella* – 25 – 1 – 43 – 19 ×
E – 5 – 199 *formosa* – 58 *formosa* – 14 *formosa* } 27 *formosa*
×
E – 43 – 89 – 5 – 1
(= f. *typica* C × 25 No. 27 *formosa*)

12 C – 22 – 7 – 40 – 5 – 9 – 1 ×
E – 5 – 199 *formosa* – 28 *formosa* – 62 *formosa* } 27 *formosa*

13 C – 22 – 7 – 40 – 5 – 9 – 1 ×
E – 5 – 199 *formosa* – 28 *formosa* ×
C – 22 – 13 *latifolia* – 87 *latifolia* } 162 – 164 *formosa* ×
E – 43 – 89 – 5 – 19 } 16 *formosa*
(= f. *typica* C × 23 No. 16 *formosa*)

14 C – 52 – 6 *grisella* – 25 – 1 – 43 – 18 ×
E – 5 – 199 *formosa* – 58 *formosa* – 15 *formosa* } 63 *formosa*
×
E – 43 – 89 – 5 – 1
(= f. *typica* C × 25 No. 63 *formosa*)

15 C – 22 – 7 – 40 – 5 – 9 – 2 ×
E – 5 – 199 *formosa* – 58 *formosa* – 15 *formosa* } 63 *formosa*
×
E – 43 – 89 – 5 – 1
(= f. *typica* C × 25 No. 63 *formosa*)

TABLE 1 (continued)

16 $\left.\begin{array}{l}\left.\begin{array}{l}\text{E - 5 - 199 } \textit{formosa} \text{ - 28 } \textit{formosa}\\ \times\\ \text{C - 22 - 13 } \textit{latifolia} \text{ - 87 } \textit{latifolia}\end{array}\right\} \text{162 - 164 } \textit{formosa}\\ \times\\ \text{E - 43 - 89 - 5 - 19}\end{array}\right\} \times \left.\begin{array}{l}\text{C - 22 - 7 - 40 - 5 - 9 - 2}\\ \times\\ \text{3 } \textit{formosa}\end{array}\right\}$

(= f. *typica* C × 23 No. 3 *formosa*)

17 $\left.\begin{array}{l}\text{E - 5 - 199 } \textit{formosa} \text{ - 58 } \textit{formosa} \text{ - 35 } \textit{formosa}\\ \times\\ \text{E - 43 - 89 - 5 - 19}\end{array}\right\}$

18 $\left.\begin{array}{l}\left.\begin{array}{l}\text{E - 5 - 199 } \textit{formosa} \text{ - 28 } \textit{formosa}\\ \times\\ \text{C - 22 - 13 } \textit{latifolia} \text{ - 87 } \textit{latifolia}\end{array}\right\} \text{162 - 153 } \textit{formosa}\\ \times\\ \text{E - 43 - 72 - 5 - 6}\end{array}\right\}$

(= 3 No. 153 *formosa* × f. *typica* E)

19 $\left.\begin{array}{l}\left.\begin{array}{l}\text{E - 5 - 199 } \textit{formosa} \text{ - 28 } \textit{formosa}\\ \times\\ \text{C - 22 - 13 } \textit{latifolia} \text{ - 87 } \textit{latifolia}\end{array}\right\} \text{162 - 138 } \textit{formosa}\\ \times\\ \text{E - 43 - 72 - 5 - 6}\end{array}\right\}$

(= 3 No. 138 *formosa* × f. *typica* E)

20 $\left.\begin{array}{l}\left.\begin{array}{l}\text{E - 5 - 199 } \textit{formosa} \text{ - 28 } \textit{formosa}\\ \times\\ \text{C - 22 - 13 } \textit{latifolia} \text{ - 87 } \textit{latifolia}\end{array}\right\} \text{162 - 164 } \textit{formosa}\\ \times\\ \text{E - 43 - 72 - 5 - 6}\end{array}\right\}$

(= 3 No. 164 *formosa* × f. *typica* E)

21 $\left.\begin{array}{l}\left.\begin{array}{l}\text{E - 5 - 199 } \textit{formosa} \text{ - 28 } \textit{formosa}\\ \times\\ \text{C - 22 - 13 } \textit{latifolia} \text{ - 87 } \textit{latifolia}\end{array}\right\} \text{162 - 30 } \textit{formosa}\\ \times\\ \text{E - 43 - 89 - 5 - 1}\end{array}\right\}$

(= 3 No. 30 *formosa* × f. *typica* E)

22 $\left.\begin{array}{l}\text{E - 5 - 199 } \textit{formosa} \text{ - 58 } \textit{formosa} \text{ - 14 } \textit{formosa}\\ \times\\ \text{E - 43 - 89 - 5 - 1}\end{array}\right\}$

23 $\left.\begin{array}{l}\left.\begin{array}{l}\text{E - 5 - 199 } \textit{formosa} \text{ - 28 } \textit{formosa}\\ \times\\ \text{C - 22 - 13 } \textit{latifolia} \text{ - 87 } \textit{latifolia}\end{array}\right\} \text{162 - 164 } \textit{formosa}\\ \times\\ \text{E - 43 - 89 - 5 - 19}\end{array}\right\}$

(= 3 No. 164 *formosa* × f. *typica* E)

24 $\left.\begin{array}{l}\left.\begin{array}{l}\text{E - 5 - 199 } \textit{formosa} \text{ - 28 } \textit{formosa}\\ \times\\ \text{C - 22 - 13 } \textit{latifolia} \text{ - 87 } \textit{latifolia}\end{array}\right\} \text{4 - 22 } \textit{formosa}\\ \times\\ \text{E - 43 - 89 - 5 - 19}\end{array}\right\}$

(= 1 No. 22 *formosa* × f. *typica* E)

TABLE 1 (continued)

25 E – 5 – 199 *formosa* – 58 *formosa* – 15 *formosa* × E – 43 – 89 – 5 – 1

26 E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia* → 162 – 138 *formosa* × E – 43 – 72 – 5 – 6 → 21 *formosa* × (E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia*) → 190 – 4 – 16
(= 19 No. 21 *formosa* × 2 No. 4 – 16 f. *typica* M (homozygous))

27 E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia* → 162 – 138 *formosa* × E – 43 – 72 – 5 – 6 → 14 *formosa* × (E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia*) → 190 – 4 – 21
(= 19 No. 14 *formosa* × 2 No. 4 – 21 f. *typica* M (homozygous))

28 E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia* → 162 – 153 *formosa* × E – 43 – 72 – 5 – 6 → 8 *formosa* × (E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia*) → 190 – 4 – 1
(= 18 No. 8 *formosa* × 2 No. 4 – 1 f. *typica* M (homozygous))

29 E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia* → 162 – 153 *formosa* × E – 43 – 72 – 5 – 6 → 10 *formosa* × (E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia*) → 190 – 4 – 10
(= 18 No. 10 *formosa* × 2 No. 4 – 10 f. *typica* M (homozygous))

30 E – 5 – 199 *formosa* – 58 *formosa* – 15 *formosa* × E – 43 – 89 – 5 – 1 → 69 *formosa* × (E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia*) → 190 – 4 – 16
(= 25 No. 69 *formosa* × 2 No. 4 – 16 f. *typica* M (homozygous))

TABLE 1 (continued)

31 E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia*; 4 – 164b × E – 43 – 89 – 5 – 1; 2 *formosa*; E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia*; 190 – 54 – 6

(= 55 No. 2 *formosa* × 2 No. 54 – 6 f. *typica* M (homozygous))

32 E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia*; 190 – 54 – 3; E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia*; 4 – 164b × E – 43 – 89 – 5 – 1; 1 *formosa*

(= 2 No. 54 – 3 f. *typica* M (homozygous) × 55 No. 1 *formosa*)

33 E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia*; 190 – 54 – 6; E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia*; 4 – 164b × E – 43 – 89 – 5 – 1; 1 *formosa*

(= 2 No. 54 – 6 f. *typica* M (homozygous) × 55 No. 1 *formosa*)

34 E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia*; 190 – 4 – 6; E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia*; 4 – 22 *formosa* × E – 43 – 89 – 5 – 19; 13 *formosa*

(= 2 No. 4 – 6 f. *typica* M (homozygous) × 24 No. 13 *formosa*)

35 E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia*; 190 – 4 – 10; E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia*; 162 – 153 *formosa* × E – 43 – 72 – 5 – 6; 10 *formosa*

(= 2 No. 4 – 10 f. *typica* M (homozygous) × 18 No. 10 *formosa*)

TABLE 1 (continued)

36 (E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia*) 190 – 4 – 15 × (E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia*) 162 – 153 *formosa* × E – 43 – 72 – 5 – 6) 10 *formosa*

(= 2 No. 4 – 15 f. *typica* M (homozygous) × 18 No. 10 *formosa*)

37 (E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia*) 190 – 4 – 2 × (E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia*) 162 – 153 *formosa* × E – 43 – 72 – 5 – 6) 10 *formosa*

(= 2 No. 4 – 2 f. *typica* M (homozygous) × 18 No. 10 *formosa*)

38 (E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia*) 190 – 4 – 21 × (E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia*) 162 – 153 *formosa* × E – 43 – 72 – 5 – 6) 10 *formosa*

(= 2 No. 4 – 21 f. *typica* M (homozygous) × 18 No. 10 *formosa*)

39 (E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia*) 4 – 176 – 1 × (E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia*) 162 – 30 *formosa* × E – 43 – 89 – 5 – 1) 9 *formosa*

(= 1 No. 176 – 1 f. *typica* M (homozygous) × 21 No. 9 *formosa*)

40 (E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia*) 4 – 176 – 13 × (E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia*) 162 – 30 *formosa* × E – 43 – 89 – 5 – 1) 9 *formosa*

(= 1 No. 176 – 13 f. *typica* M (homozygous) × 21 No. 9 *formosa*)

41 (E – 5 – 199 *formosa* – 28 *formosa* – 31 *formosa* × E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia*) 4 – 62

(= *formosa* × 1 No. 62 f. *typica* M (heterozygous))

TABLE 1 (continued)

42 E – 5 – 199 *formosa* – 58 *formosa* – 15 *formosa* × E – 43 – 89 – 5 – 1 } 68 *formosa* × E – 5 – 199 *formosa* – 58 *formosa* – 44 *formosa* × CD – 9 *viscida*[4] – 26 *viscida* – 11 *viscida* – 24 *viscida* } 6 *viscida*
(= 25 No. 68 *formosa* × *viscida* M (heterozygous))

43 E – 5 – 199 *formosa* – 58 *formosa* – 15 *formosa* × E – 43 – 89 – 5 – 1 } 68 *formosa* × E – 5 – 199 *formosa* – 58 *formosa* – 12 *formosa* × CD – 9 *viscida* – 26 *viscida* – 11 *viscida* – 24 *viscida* } 1 *viscida*
(= 25 No. 68 *formosa* × *viscida* M (heterozygous))

44 E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia* } 4 – 165 × E – 5 – 199 *formosa* – 28 *formosa* – 62 *formosa*
(= 1 No. 165 f. *typica* M (heterozygous) × *formosa*)

45 E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia* } 4 – 164b × E – 5 – 199 *formosa* – 28 *formosa* – 31 *formosa*
(= 1 No. 164b f. *typica* M (heterozygous) × *formosa*)

46 E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia* } 4 – 163b × E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia* } 4 – 33 *formosa*
(= 1 No. 163b f. *typica* M (heterozygous) × 1 No. 33 *formosa*)

47 E – 43 – 89 – 5 – 1 – 2 × E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia* } 190 – 4 – 2
(= f. *typica* E × 2 No. 4 – 2 f. *typica* M (homozygous))

48 E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia* } 4 – 64 – 9 × E – 43 – 74 – 41 – 45 – 2
(= 1 No. 64 – 9 f. *typica* M (homozygous) × f. *typica* E)

[4] A hybrid of *Oenothera pratincola* × *Oe. numismatica* (BARTLETT 1915a, p. 86). This form is like *Oe. pratincola* f. *typica* with the addition of the viscid pubescence of *Oe. numismatica*.

TABLE 1 (continued)

49 E – 5 – 199 *formosa* – 28 *formosa* } 190 – 4 – 6
× } ×
C – 22 – 13 *latifolia* – 87 *latifolia* } E – 43 – 74 – 21 – 3
(= 2 No. 4 – 6 f. *typica* M (homozygous) × f. *typica* E)

50 E – 5 – 199 *formosa* – 28 *formosa* } 190 – 54 – 2
× } ×
C – 22 – 13 *latifolia* – 87 *latifolia* } E – 43 – 72 – 5 – 6 – 12
(= 2 No. 54 – 2 f. *typica* M (homozygous) × f. *typica* E)

51 E – 5 – 199 *formosa* – 28 *formosa* } 190 – 4 – 2
× } ×
C – 22 – 13 *latifolia* – 87 *latifolia* } E – 43 – 89 – 5 – 1 – 6
(= 2 No. 4 – 2 f. *typica* M (homozygous) × f. *typica* E)

52 E – 5 – 199 *formosa* – 28 *formosa* } 4 – 176 – 1
× } ×
C – 22 – 13 *latifolia* – 87 *latifolia* } E – 43 – 74 – 21 – 3
(= 1 No. 176 – 1 f. *typica* M (homozygous) × f. *typica* E)

53 E – 5 – 199 *formosa* – 28 *formosa* } 4 – 176
× } ×
C – 22 – 13 *latifolia* – 87 *latifolia* } E – 43 – 72 – 5 – 6
(= 1 No. 176 f. *typica* M (homozygous) × f. *typica* E)

54 E – 5 – 199 *formosa* – 28 *formosa* } 4 – 165
× } ×
C – 22 – 13 *latifolia* – 87 *latifolia* } E – 43 – 89 – 5 – 1
(= 1 No. 165 f. *typica* M (heterozygous) × f. *typica* E)

55 E – 5 – 199 *formosa* – 28 *formosa* } 4 – 164b
× } ×
C – 22 – 13 *latifolia* – 87 *latifolia* } E – 43 – 89 – 5 – 1
(= 1 No. 164b f. *typica* M (heterozygous) × f. *typica* E)

56 E – 5 – 199 *formosa* – 28 *formosa* } 4 – 163b
× } ×
C – 22 – 13 *latifolia* – 87 *latifolia* } E – 43 – 89 – 5 – 1
(= 1 No. 163b f. *typica* M (heterozygous) × f. *typica* E)

TABLE 1 (continued)

57 E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia* } 4 – 167b × E – 43 – 89 – 5 – 19 }
(= 1 No. 167b f. *typica* M (heterozygous) × f. *typica* E)

58 E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia* } 190 – 4 – 6 × C – 52 – 6 – 25 – 1 – 43 – 2 }
(= 2 No. 4 – 6 f. *typica* M (homozygous) × f. *typica* C)

59 E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia* } 4 – 176 × C – 22 – 7 – 40 – 5 – 2 }
(= 1 No. 176 f. *typica* M (homozygous) × f. *typica* C)

60 E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia* } 4 – 167b × C – 22 – 7 – 40 – 5 – 2 }
(= 1 No. 167b f. *typica* M (heterozygous) × f. *typica* C)

61 E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia* } 4 – 165 × C – 22 – 7 – 40 – 5 – 2 }
(= 1 No. 165 f. *typica* M (heterozygous) × f. *typica* C)

62 E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia* } 4 – 163b × C – 22 – 7 – 40 – 5 – 2 }
(= 1 No. 163b f. *typica* M (heterozygous) × f. *typica* C)

63 E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia* } 4 – 186 *formosa* × E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia* } 4 – 166 }
(= 1 No. 186 *formosa* × 1 No. 166 f. *typica* M (homozygous))

64 E – 5 – 199 *formosa* – 58 *formosa* – 15 *formosa* × E – 43 – 89 – 5 – 1 } 69 *formosa* × E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia* } 190 – 4 – 16 }
(= 25 No. 69 *formosa* × 2 No. 4 – 16 f. *typica* M (homozygous))

TABLE 1 (concluded)

65 E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia* } 190 – 4 – 16 × E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia* } 162 – 153 *formosa* × E – 43 – 72 – 5 – 6 } x *formosa*

(= 2 No. 4 – 16 f. *typica* M (homozygous) × 18 No. x *formosa*)

66 E – 5 – 199 *formosa* – 28 *formosa* × C – 22 – 13 *latifolia* – 87 *latifolia* } 4 – 176 × E – 5 – 208 *angustifolia* – 1 *nitidissima*[5] – 15 *formosa*

(= 1 No. 176 f. *typica* M (homozygous) × *formosa*)

[5] See BARTLETT 1915b, p. 440, table IV.

TABLE 2

A classification of the F_3 generation resulting from self-pollination of normal f. typica plants chosen at random from the segregating F_2 generation of the cross mut. formosa × mut. latifolia C. (Male gametes of mut. latifolia are the same as those of f. typica of the strain from which it arose).

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
1	No. 16	370	57	42	15	2.80:1
1	No. 19	319	70	64	6	10.67:1
1	No. 20	598	22	19	3	6.33:1
1	No. 24	492	140	112	28	4.00:1
1	No. 26	448	57	45	12	3.75:1
1	No. 28	543	40	30	10	3.00:1
1	No. 29	578	78	62	16	3.88:1
1	No. 32	514	44	36	8	4.50:1
1	No. 37	243	62	42	20	2.10:1
1	No. 43	368	98	77	21	3.67:1
1	No. 44	299	62	53	9	5.89:1
1	No. 47	433	132	99	33	3.00:1
1	No. 62	209	162	125	37	3.38:1
1	No. 154a	227	56	38	18	2.11:1
1	No. 155a	316	63	40	23	1.74:1
1	No. 156	173	43	32	11	2.91:1
1	No. 158	278	104	84	20	4.20:1
1	No. 161	589	99	74	25	2.96:1
1	No. 163b	1,300	48	39	9	4.33:1
1	No. 164b	1,358	229	172	57	3.02:1
1	No. 167a	230	47	39	8	4.88:1
1	No. 167b	2,383	246	203	43	4.72:1
1	No. 168	598	129	95	34	2.80:1
1	No. 171	270	108	77	31	2.48:1
1	No. 175	518	123	93	30	3.10:1
1	No. 177a	178	42	32	10	3.20:1
2	No. 8	255	24	22	2	11.00:1
2	No. 9	338	35	26	9	2.89:1
2	No. 16	517	27	22	5	4.40:1
2	No. 18	506	23	15	8	1.87:1
2	No. 64	545	58	38	20	1.90:1
2	No. 65	562	107	73	34	2.15:1
2	No. 70	334	23	17	6	2.83:1
2	No. 73	567	161	105	56	1.87:1
3	No. 38	350	52	37	15	2.47:1
3	No. 72	472	55	46	9	5.11:1
3	No. 170	343	85	61	24	2.54:1
3	No. 183	491	33	20	13	1.54:1
3	No. 190	455	54	33	21	1.57:1
3	No. 198	215	21	10	11	0.91:1
3	No. 215	460	39	35	4	8.75:1
Total.....		20,242	3,158	2,384	774	3.08:1

TABLE 2 (continued)

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
1	No. 15	179	25	25	0	
1	No. 17	437	58	58	0	
1	No. 35	441	91	91	0	
1	No. 36	493	42	42	0	
1	No. 39	379	61	61	0	
1	No. 49	370	120	120	0	
1	No. 64	371	166	166	0	
1	No. 125	401	112	112	0	
1	No. 160a	436	47	47	0	
1	No. 164a	495	116	116	0	
1	No. 166	582	60	60	0	
1	No. 176	1,341	191	191	0	
2	No. 4	220	130	130	0	
2	No. 5	393	112	112	0	
2	No. 6	243	30	30	0	
2	No. 17	250	51	51	0	
2	No. 19	229	89	89	0	
2	No. 54	534	219	219	0	
2	No. 67	595	124	124	0	
3	No. 75	554	239	239	0	
3	No. 107	306	34	34	0	
3	No. 169	416	48	48	0	
Total.....		9,665	2,165	2,165	0	

This table shows the presence of homozygous and heterozygous dominants in the F_2 generation. The ratio of non-segregating to segregating cultures in this table is 22:41, which closely approximates the expected ratio, 1:2, of homozygous to heterozygous dominants in the F_2 generation.

TABLE 3

Analysis of the F_4 generation resulting from self-pollination of f. typica plants chosen at random from the non-segregating F_3 progenies (see table 2) of the cross mut. formosa × mut. latifolia C.

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
1	No. 39–14	ca. 1,300†[6]	254	254	0	
1	No. 39–24	ca. 1,100†	167	167	0	
1	No. 64–9	ca. 1,000†	109	109	0	
1	No. 125–44	ca. 750†	18	18	0	
1	No. 125–46	ca. 900†	85	85	0	
1	No. 125–48	ca. 800†	14	14	0	
1	No. 125–49	ca. 850†	26	26	0	
1	No. 166–9	ca. 1,200†	10	10	0	
1	No. 176–1	ca. 700†	20	20	0	
1	No. 176–13	ca. 900†	51	51	0	
2	No. 4–2	ca. 900†	47	47	0	
2	No. 4–3	ca. 800†	78	78	0	
2	No. 4–6	ca. 700†	15	15	0	
2	No. 4–16	ca. 1,200†	138	138	0	
2	No. 4–21	ca. 700†	69	69	0	
2	No. 54–6	ca. 600†	13	13	0	
Total.....		ca. 14,400	1,114	1,114	0	

All of the plants are flat-leaved, demonstrating further the presence of homozygous dominants in the F_2 generation of the cross. Of the 326 plants grown to maturity, taken in part from each of twelve cultures, 320 proved to be f. *typica* and of the remaining 6 plants 2 were mut. *nummularia*,[7] 2 were mut. *fallax*, an undescribed mutation, as a seedling very much like mut. *nummularia* and thrown by the same strains, 1 was probably mut. *gigas*,[8] and 1 resembled mut. *angustifolia*.[9]

TABLE 4

Analysis of the F_4 generation resulting from self-pollination of f. typica plants chosen at random from the segregating F_3 progenies (see table 2) of the cross mut. formosa × mut. latifolia C.

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
1	No. 167b–12	ca. 550†	15	10	5	2.00:1
1	No. 167b–25	ca. 900†	165	132	33	4.00:1
Total.....		ca. 1,450†	180	142	38	3.74:1
1	No. 168–44	ca. 700†	25	25	0	

Of the three cultures, two are segregating and one is not, showing the presence of homozygous and heterozygous dominants in the F_3 generation from heterozygous F_2 plants. Of the 64 plants grown to maturity from the two segregating cultures 52 proved to be f. *typica*, 1 was mut. *fallax*, 10 were mut. *formosa*, and 1 was mut. *setacea*,[10] which is a revolute-leaved type thrown by mut. *formosa*. All of the 25 plants of the non-segregating culture proved to be f. *typica*.

[6] In this and subsequent tables the dagger (†) indicates that seeds from two or more capsules were sown together.

[7] Mut. *nummularia*, a mutation commonly thrown by strain C, but never by pure strain E See BARTLETT 1915 a, p. 97; COBB and BARTLETT 1919.

[8] See BARTLETT, 1915 b, p. 443.

[9] See BARTLETT, 1915 b, p. 438.

[10] See BARTLETT, 1915 b, p. 450.

TABLE 5

Analysis of the F_1 generation of the cross mut. formosa × f. typica C ($\alpha'\beta ff \times \alpha\beta FF$).

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
4		ca. 300†	7	7	0	
5		316†	10	10	0	
6		51*[11]	8	8	0	
7		327†	28	28	0	
8		57†	30	30	0	
9		33*	17	17	0	
Total.....		1,084	100	100	0	

The cultures consist of flat-leaved types only, but as seedlings the plants show the effect of crossing in irregularities in their leaves, the blades being unsymmetrically developed. Of the 95 plants grown to maturity, taken in part from each of the six cultures, all proved to be f. *typica* except 1 plant, which was an undescribed flat-leaved mutation, mut. *dimorpha*.

TABLE 6

Analysis of the F_2 generation resulting from self-pollination of f. typica plants chosen at random from the F_1 generation (see table 5) of the cross mut. formosa × f. typica C ($\alpha'\beta ff \times \alpha\beta FF$). Each of the cultures contains both flat-leaved and revolute-leaved plants in approximately a 3:1 ratio.

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
4	No. 3	ca. 500†	165	132	33	4.00:1
4	No. 5	ca. 850†	67	54	13	4.15:1
4	No. 6	ca. 900†	452	337	115	2.93:1
5	No. 7	ca. 700†	87	69	18	3.83:1
5	No. 9	ca. 800†	346	243	103	2.36:1
6	No. 1	ca. 600†	208	155	53	2.92:1
6	No. 3	ca. 800†	121	86	35	2.46:1
6	No. 6	ca. 1,000†	111	81	30	2.70:1
6	No. 7	ca. 1,000†	483	347	136	2.55:1
6	No. 8	ca. 900†	244	181	63	2.87:1
7	No. 4	ca. 800†	286	220	66	3.33:1
7	No. 6	ca. 900†	202	141	61	2.31:1
7	No. 9	ca. 900†	182	120	62	1.94:1
7	No. 10	ca. 900†	200	146	54	2.70:1
8	No. 10	ca. 950†	120	87	33	2.64:1
Total.....		ca. 12,500	3,274	2,399	875	2.74:1

[11] The asterisk (*) in this and subsequent tables indicates that seeds from a single capsule were sown.

TABLE 7

Analysis of the F_1 generation of the cross f. typica C × mut. formosa ($\alpha\beta FF \times \alpha'\beta ff$).

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
10		100†	63	63	0	
11		221*	50	50	0	
12		140*	88	88	0	
13		*	45	45	0	
14		186*	125	125	0	
15		†	176	176	0	
16		300†	235	235	0	
Total.....		947+	782	782	0	

The cultures consist of flat-leaved types only. Of the 389 plants grown to maturity, taken in part from each of the seven cultures, 381 were f. *typica*, and the remaining 8 were of other flat-leaved types—3 of mut. *fallax*, 2 of mut. *dimorpha*, 1 of mut. *grisella* (an undescribed mutation), and 2 undetermined mutations.

TABLE 8

Analysis of the F_2 generation resulting from self-pollination of f. typica plants chosen at random from the F_1 generation (see table 7) of the cross f. typica C × mut. formosa ($\alpha\beta FF \times \alpha'\beta ff$).

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
10	No. 1	1,296†	545	533	12	
10	No. 2	1,425†	92	92	0	
10	No. 17	810†	174	174	0	
10	No. 25	681†	18	17	1	
10	No. 42	1,113†	142	142	0	
11	No. 32	1,265†	41	41	0	
11	No. 35	1,243†	17	16	1	
11	No. 37	1,428†	29	26	3	
11	No. 44	1,812†	8	7	1	
11	No. 50	1,574†	57	54	3	
12	No. 12	1,455†	3	2	1	
12	No. 14	1,693†	127	126	1	
12	No. 29	1,594†	5	4	1	
12	No. 36	1,214†	87	86	1	
12	No. 44	1,232†	309	308	1	
Total.....		19,835	1,654	1,628	26	61.5:1

The cultures consist of flat-leaved plants with a small percentage of revolute-leaved plants, considered to have arisen by separate mutations of the α gamete in the presence of the recessive allelomorphs of the Mendelian factors for flatness.

TABLE 9

Analysis of the F_1 generation of the cross mut. formosa × f. typica E ($\alpha'\beta ff \times \alpha\beta ff$).

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
17		258†	21	0	21	
18		471†	10	0	10	
19		535†	86	0	86	
20		157*	10	0	10	
21		150*	13	0	13	
22		167*	33	0	33	
23		100*	21	0	21	
24		138*	25	0	25	
25		866†	86	0	86	
Total.....		2,842	305	0	305	

All of the plants are revolute-leaved. Of the 235 plants grown to maturity, taken in part from each of the nine cultures, 230 were mut. *formosa*, and the remaining 5 were plants of other revolute-leaved types—3 of mut. *revoluta*,[12] 1 of mut. *setacea*, and 1 of mut. *albicans* (?),[13] all of these being types thrown by pure strains of mut. *formosa*.

TABLE 10

Analysis of the F_2 generation resulting from self-pollination of f. typica plants chosen at random from the F_1 generation (see table 9) of the cross mut. formosa × f. typica E ($\alpha'\beta ff \times \alpha\beta ff$).

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
22	No. 24	ca. 800†	260	0	260	
23	No. 2	ca. 600†	111	0	111	
25	No. 63	ca. 800†	216	0	216	
18	No. 8	ca. 750†	41	0	41	
Total.....		ca. 2,950	628	0	628	

All of the plants are revolute-leaved, as in the F_1 generation of this cross; that is, the inheritance is matroclinic. Of the 72 plants grown to maturity, taken in part from each of the four cultures, all proved to be mut. *formosa*.

[12] See BARTLETT, 1915b, p. 450.

[13] See BARTLETT, 1915b, p. 449.

TABLE 11

Analysis of the F_1 generation of the cross mut. formosa × f. typica M (homozygous) ($\alpha'\beta ff \times \alpha'\beta FF$). The staminate parent belonged to the F_2 generation of the cross mut. formosa × mut. latifolia C.

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
26		153†	113	113	0	
27		225†	69	69	0	
28		56*	12	12	0	
29		79*	30	30	0	
30		152†	26	26	0	
31		167†	42	42	0	
Total.....		832	292	292	0	

Each culture contains only flat-leaved plants. Of the 181 plants grown to maturity, taken in part from each of the six cultures, 160 proved to be f. *typica*, and the remaining 21 were of other flat-leaved types—16 were mut. *dimorpha*, 1 was mut. *fallax*, 1 was mut. *grisea* (an undescribed mutation), and 3 were undetermined.

TABLE 12

Analysis of the F_2 generation resulting from self-pollination of f. typica plants chosen at random from the F_1 generation (see table 11) of the cross mut. formosa × f. typica M (homozygous) ($\alpha'\beta ff \times \alpha'\beta FF$). Each of the cultures contains flat-leaved and revolute-leaved plants in approximately a 3:1 ratio.

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
26	No. 41	ca. 1,400†	95	71	24	2.96:1
26	No. 3	ca. 2,000†	245	166	79	2.10:1
26	No. 9	ca. 1,200†	62	46	16	2.87:1
26	No. 25	ca. 1,200†	34	23	11	2.09:1
26	No. 46	ca. 2,100†	61	39	22	1.77:1
27	No. 3	ca. 2,200†	31	22	9	2.44:1
27	No. 15	ca. 2,050†	23	20	3	6.67:1
27	No. 16	ca. 2,050†	51	32	19	1.68:1
27	No. 20	ca. 2,100†	28	21	7	3.00:1
29	No. 6	ca. 1,500†	73	54	19	2.84:1
29	No. 12	ca. 1,150†	25	20	5	4.00:1
29	No. 16	ca. 1,100†	282	216	66	3.27:1
29	No. 18	ca. 1,650†	112	84	28	3.00:1
29	No. 25	ca. 1,650†	120	68	52	1.31:1
31	No. 4	ca. 1,800†	126	92	34	2.71:1
31	No. 6	ca. 1,900†	86	56	30	1.87:1
63	No. 1	ca. 8,900†	993	742	251	2.96:1
63	No. 2	ca. 4,600†	849	655	194	3.38:1
63	No. 3	ca. 1,450†	563	423	140	3.02:1
63	No. 4	ca. 1,500†	77	59	18	3.28:1
64	No. 13	ca. 2,300†	81	62	19	3.26:1
64	No. 15	ca. 2,500†	229	158	71	2.23:1
64	No. 17	ca. 2,100†	73	46	27	1.70:1
64	No. 23	ca. 2,000†	300	212	88	2.41:1
64	No. 24	ca. 2,300†	718	508	210	2.42:1
Total.....		ca. 54,700	5,337	3,895	1,442	2.70:1

TABLE 13

Analysis of the F_1 generation of the cross f. typica M (homozygous) × mut. formosa ($\alpha'\beta FF \times \alpha'\beta ff$).

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
32		ca. 300†	48	48	0	
33		293†	122	122	0	
34		202†	18	18	0	
35		220†	27	27	0	
36		50*	33	33	0	
37		66†	45	45	0	
38		204†	122	122	0	
39		182†	23	23	0	
40		71†	36	36	0	
Total.....		ca. 1,588	474	474	0	

The pistillate parent belonged to the F_2 generation of the cross mut. *formosa* × mut. *latifolia* C. Each of the cultures consists of only flat-leaved plants. Of the 210 plants grown to maturity, taken in part from each of the nine cultures, 204 proved to be f. *typica*, and the remaining 6 were of other flat-leaved types,—3 were mut. *dimorpha*, 1 was mut. *fallax*, 1 was mut. *sub-latifolia* (?),[14] and 1 was undetermined.

TABLE 14

Analysis of the F_2 generation resulting from self-pollination of f. typica plants chosen at random from the F_1 generation (see table 13) of the cross f. typica M (homozygous) × mut. formosa ($\alpha'\beta FF \times \alpha'\beta ff$).

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
32	No. 3	ca. 1,750†	64	46	18	2.56:1
32	No. 4	ca. 1,700†	203	155	48	3.23:1
34	No. 7	ca. 1,900†	122	92	30	3.07:1
34	No. 9	ca. 1,650†	78	63	15	4.20:1
34	No. 13	ca. 1,950†	739	549	190	2.89:1
35	No. 4	ca. 1,600†	111	72	39	1.85:1
35	No. 7	ca. 1,275†	556	406	150	2.71:1
35	No. 11	ca. 1,600†	34	23	11	2.09:1
37	No. 11	ca. 2,150†	147	109	38	2.87:1
37	No. 16	1,353†	38	31	7	4.43:1
37	No. 21	ca. 1,850†	159	120	39	3.08:1
37	No. 23	1,103†	54	40	14	2.86:1
38	No. 5	ca. 1,900†	110	78	32	2.44:1
38	No. 6	ca. 1,900†	380	283	97	2.92:1
38	No. 24	ca. 2,600†	443	312	131	2.38:1
65	No. 1	ca. 1,400†	210	143	67	2.13:1
65	No. 4	ca. 1,450†	159	109	50	2.18:1
66	No. 1	ca. 700†	225	150	75	2.00:1
66	No. 2	ca. 700†	34	26	8	3.25:1
66	No. 3	ca. 1,600†	434	313	121	2.59:1
Total.....		ca. 32,131	4,300	3,120	1,180	2.64:1

Each of the cultures contains both flat-leaved and revolute-leaved plants, in approximately a 3:1 ratio. Of the 74 plants from three of these cultures, grown to maturity, 58 proved to be f. *typica* and 16 proved to be mut. *formosa*.

[14] An undescribed mutation.

TABLE 15

Analysis of the F_1 generation of the cross mut. formosa × f. typica M (heterozygous) ($\alpha'\beta ff \times \alpha'\beta Ff$).

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
41		333†	13	5	8	0.63:1
42		64*	27	15	12	1.25:1
43		40*	19	7	12	0.58:1
Total.....		437	59	27	32	0.84:1

In the case of **41**, the staminate parent belonged to the F_2 generation of the cross mut. *formosa* × mut. *latifolia* C; in the case of **42** and **43** to the F_2 generation of the cross mut. *formosa* × hyb. *viscida*.[15] In each of the cultures flat-leaved and revolute-leaved plants occur, in about equal numbers. The expected ratio is 1:1. When the germination is poor, the number of revolute-leaved plants often slightly exceeds the expectation, as it does here. Of the 42 plants grown to maturity, taken in part from each of the three cultures, 21 were f. *typica* (one of them a dwarf), 3 were of other flat-leaved types (2 of mut. *graminea*,[16] and 1 an undetermined mutation), 16 were mut. *formosa* (6 of them very poor plants) and 2 were mut. *revoluta*, which is one of the revolute-leaved mutations thrown by mut. *formosa*.

TABLE 16

Analysis of an F_2 progeny resulting from self-pollination of an f. typica plant of the F_1 generation (see table 15) of the cross mut. formosa × f. typica M (heterozygous) ($\alpha'\beta ff \times \alpha'\beta Ff$). The numbers of flat-leaved and revolute-leaved plants closely approximate a 3:1 ratio.

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
41	No. 10	ca. 4,250†	1,849	1,348	501	2.69:1

TABLE 17

Analysis of the F_1 generation of the cross f. typica M (heterozygous) × mut. formosa ($\alpha'\beta Ff \times \alpha'\beta ff$).

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
44		657†	117	58	59	1.98:1
45		319†	50	20	30	0.67:1
Total.....		976	167	78	89	0.88:1

The pistillate parent belonged to the F_2 generation of the cross mut. *formosa* × mut. *latifolia* C. In these cultures flat-leaved and revolute-leaved plants occur in about equal numbers, but, as in the reciprocal cross, the number of revolute-leaved plants slightly exceeds that required for the expected 1:1 ratio. Of the 88 plants grown to maturity, taken in part from each of the two cultures, 36 were f. *typica*, 2 were of other flat-leaved types (1 of mut. *ericacea*[17] and 1 dwarf), and 50 were mut. *formosa*, one of them bearing a flat-leaved bud-sport.

[15] Hyb. *viscida*, a hybrid of *Oenothera pratincola* × *Oe. numismatica* (see BARTLETT 1915 a, p. 86). This form is like *Oe. pratincola* f. *typica* with the addition of the viscid pubescence of *Oe. numismatica*.

[16] Regarding mut. *graminea*, see BARTLETT 1915 b, p. 429.

[17] An undescribed mutation.

TABLE 18

Analysis of the F_2 generation resulting from self-pollination of f. typica plants chosen at random from the F_1 generation (see table 17) of the cross f. typica M (heterozygous) × mut. formosa ($\alpha'\beta Ff \times \alpha'\beta ff$).

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
45	No. 12	ca. 750†	157	114	43	2.65:1
46	No. 2	ca. 600†	22	16	6	2.66:1
44	No. 14	ca. 900†	18	14	4	3.50:1
44	No. 17	ca. 800†	463	344	119	2.89:1
Total.....		ca. 3,050	660	488	172	2.84:1

Each of the cultures contains both flat-leaved and revolute-leaved plants, in approximately a 3:1 ratio. Of the 50 plants from one culture grown to maturity, 42 proved to be f. *typica* and 8 proved to be mut. *formosa*.

TABLE 19

Analysis of an F_1 progeny of the cross f. typica E × f. typica M (homozygous) ($\alpha\beta ff \times \alpha'\beta FF$).

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
47		95†	78	78	0	

The staminate parent belonged to the F_2 generation of the cross mut. *formosa* × mut. *latifolia* C. All of the plants are flat-leaved. Of the 49 plants grown to maturity, 44 were f. *typica*, and the remaining 5 were of other flat-leaved types—2 of mut. *ericacea*, 2 of mut. *dimorpha*, and 1 undetermined mutation.

TABLE 20

Analysis of the F_2 generation resulting from self-pollination of f. typica plants chosen at random from the F_1 generation (see table 19) of the cross f. typica E × f. typica M (homozygous) ($\alpha\beta ff \times \alpha'\beta FF$). In each culture all of the plants are flat-leaved.

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
47	No. 4	ca. 1,700†	1,016	1,016	0	
47	No. 8	ca. 1,800†	1,265	1,265	0	
47	No. 11	ca. 1,000†	813	813	0	
47	No. 15	1,205†	91	91	0	
47	No. 19	ca. 1,400†	1,140	1,140	0	
47	No. 26	1,436†	1,062	1,062	0	
47	No. 28	ca. 1,500†	533	533	0	
47	No. 30	1,214†	169	169	0	
Total.....		ca. 11,255	6,089	6,089	0	

TABLE 21

Analysis of the F_1 generation of the cross f. typica M (homozygous) × f. typica E ($\alpha'\beta FF \times \alpha\beta ff$).

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
48		194†	21	21	0	
49		392†	238	238	0	
50		197†	128	128	0	
51		361†	275	275	0	
52		50†	32	32	0	
Total.....		1,194	694	694	0	

The pistillate parent belonged to the F_2 generation of the cross mut. *formosa* × mut. *latifolia* C. Each of the cultures contains only flat-leaved plants. Of the 157 plants grown to maturity, taken in part from each of the five cultures, 155 proved to be f. *typica*, and the remaining 2 were mut. *fallax*.

TABLE 22

Analysis of the F_2 generation resulting from self-pollination of f. typica plants chosen at random from the F_1 generation (see table 21) of the cross f. typica M (homozygous) × f. typica E ($\alpha'\beta FF \times \alpha\beta ff$).

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
50	No. 40	1,425†	629	465	164	2.84:1
50	No. 44	1,529†	461	337	124	2.72:1
51	No. 12	1,345†	612	445	167	2.66:1
53	No. 1	ca. 1,000†	494	367	127	2.88:1
53	No. 2	ca. 900†	31	23	8	2.88:1
53	No. 3	ca. 1,000†	17	12	5	2.40:1
53	No. 4	ca. 750†	10	7	3	2.33:1
53	No. 5	ca. 400†	33	22	11	2.00:1
53	No. 6	ca. 900†	12	11	1	11.00:1
Total.....		ca. 9,249	2,299	1,689	610	2.77:1

Each of the cultures contains flat-leaved and revolute-leaved plants, in approximately a 3:1 ratio. Of the 25 plants from one culture grown to maturity, 22 proved to be f. *typica*, 1 was of another flat-leaved type (mut. *dimorpha*), and 2 were mut. *formosa*.

TABLE 23

Analysis of the F_1 generation of the cross f. typica M (heterozygous) × f. typica E ($\alpha'\beta Ff \times \alpha\beta ff$).

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
54		528†	42	20	22	0.91:1
55		401†	12	6	6	1.00:1
56		430†	86	34	52	0.65:1
57		301†	34	22	12	1.83:1
Total.....		1,660	174	82	92	0.89:1

The pistillate parent belonged to the F_2 generation of the cross mut. *formosa* × mut. *latifolia* C. In each of the cultures flat-leaved and revolute-leaved plants occur in about equal numbers. The expected ratio is 1:1. When the germination is poor, the number of revolute-leaved plants often slightly exceeds the expectation, as it does here. Of the 112 plants grown to maturity, taken in part from each of the four cultures, 56 were f. *typica*, 4 were of other flat-leaved types (1 was mut. *fallax* and 3 were of a dwarf type), 51 were mut. *formosa*, and 1 was mut. *revoluta*, which is one of the revolute-leaved mutations thrown by mut. *formosa*.

TABLE 24

Analysis of the F_2 generation resulting from self-pollination of f. typica plants chosen at random from the F_1 generation (see table 23) of the cross f. typica M (heterozygous) × f. typica E ($\alpha'\beta Ff \times \alpha\beta ff$).

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE LEAVED	RATIO
54	No. 3	ca. 900†	198	153	45	3.40:1
57	No. 20	ca. 1,000†	228	167	61	2.74:1
57	No. 22	ca. 1,000†	55	41	14	2.93:1
57	No. 24	ca. 800†	12	10	2	5.00:1
57	No. 25	ca. 500†	101	79	22	3.59:1
57	No. 28	ca. 750†	107	86	21	4.10:1
Total.....		ca. 4,950	701	536	165	3.25:1

Each of the cultures contains both flat-leaved and revolute-leaved plants in approximately a 3:1 ratio. Of the 49 plants from one culture grown to maturity, 34 proved to be f. *typica* and 15 proved to be mut. *formosa*.

TABLE 25

Analysis of the F_1 generation of the cross f. typica M (homozygous) × f. typica C ($\alpha'\beta FF \times \alpha\beta FF$).

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
58		82*	57	57	0	
59		109†	11	11	0	
Total.....		191	68	68	0	

The pistillate parent belonged to the F_2 generation (in the case of 59) and the F_3 generation (in the case of 58) of the cross mut. *formosa* × mut. *latifolia* C. All of the plants are flat-leaved, and when grown to maturity all proved to be f. *typica*.

TABLE 26

Analysis of the F_2 generation resulting from self-pollination of f. typica plants chosen at random from the F_1 generation (see table 25) of the cross f. typica M (homozygous) × f. typica C ($\alpha'\beta FF \times \alpha\beta FF$). All of the plants are flat-leaved.

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
59	No. 3	ca. 400†	3	3	0	
59	No. 7	ca. 600†	2	2	0	
58	No. 1	1,664†	9	9	0	
58	No. 2	1,500†	20	20	0	
58	No. 5	1,647†	280	280	0	
58	No. 12	1,423†	230	230	0	
Total.....		ca. 7,234	544	544	0	

TABLE 27

Analysis of the F_1 generation of the cross f. typica M (heterozygous) × f. typica C ($\alpha'\beta Ff \times \alpha\beta FF$).

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
60		225†	9	9	0	
61		247†	7	7	0	
62		318+†	50	50	0	
Total.....		790+	66	68	0	

The pistillate parent belonged to the F_2 generation of the cross mut. *formosa* × mut. *latifolia* C. Each of the cultures contains only flat-leaved plants. Of the 66 plants grown to maturity, taken in part from each of the three cultures, 65 proved to be f. *typica*, and the remaining 1 was mut. *fallax*.

TABLE 28

Analysis of the F_2 generation resulting from self-pollination of f. typica plants chosen at random from the F_1 generation (see table 27) of the cross f. typica M (heterozygous) × f. typica C ($\alpha'\beta Ff \times \alpha\beta FF$).

KEY NUMBER	PARENT PLANT	SEEDS PLANTED	TOTAL PLANTS	FLAT-LEAVED	REVOLUTE-LEAVED	RATIO
60	No. 1	ca. 1,200†	839	839	0	
60	No. 4	ca. 1,300†	887	887	0	
60	No. 5	ca. 700†	239	239	0	
60	No. 6	ca. 900†	487	487	0	
60	No. 9	ca. 1,700†	1,066	1,066	0	
61	No. 2	675†	399	399	0	
61	No. 3	ca. 1,100†	465	465	0	
62	No. 8	ca. 550†	109	109	0	
62	No. 9	ca. 800†	80	80	0	
62	No. 19	ca. 400†	52	52	0	
62	No. 33	ca. 700†	48	48	0	
Total.....		ca. 10,025	4,671	4,671	0	
60	No. 3	1,011†	286	213	73	2.92:1
60	No. 8	ca. 1,200†	378	308	70	4.40:1
61	No. 1	773†	109	88	21	4.19:1
61	No. 6	ca. 1,300†	892	698	194	3.60:1
62	No. 36	ca. 600†	20	17	3	5.67:1
61	No. 4	ca. 1,000†	561	470	91	5.16:1
61	No. 5	ca. 1,500†	1,128	830	298	2.79:1
Total.....		ca. 7,384	3,374	2,624	750	3.50:1

Of the eighteen progenies, eleven consist entirely of flat-leaved plants and seven consist of flat-leaved and revolute-leaved plants in approximately a 3:1 ratio. The ratio 11:7 does not approach as closely as expected, to the 1:1 ratio of gametes bearing the dominant factor to gametes bearing the recessive factor, produced by the heterozygous pistillate parent of the cross.

TABLE 29

A summary of tables 5 to 28 inclusive.

PARENTS		F_1 GENERATION					F_2 GENERATION				
	Constitution	Table number	Type of plants	Constitution	Total plants	Ratio flat to revolute	Table number	Type of plants	Constitution	Total plants	Ratio flat to revolute
mut. *formosa*	$\alpha'\beta ff$							flat	$\alpha'\beta FF$, $\alpha'\beta Ff$	3,274	2.75:1
×	×	5	flat	$\alpha'\beta Ff$	100		6				
f. *typica* C	$\alpha\beta FF$							revolute	$\alpha'\beta ff$		
f. *typica* C	$\alpha\beta FF$							flat	$\alpha\beta FF$, $\alpha\beta Ff$, $\alpha\beta ff$	1,628	
×	×	7	flat	$\alpha\beta Ff$	782		8				
mut. *formosa*	$\alpha'\beta ff$							revolute mut.	$\alpha'\beta ff$	26	
mut. *formosa*	$\alpha'\beta ff$										
×	×	9	revolute	$\alpha'\beta ff$	305		10	revolute	$\alpha'\beta ff$	628	
f. *typica* E	$\alpha\beta ff$										
f. *typica* E	$\alpha\beta ff$	(See COBB and BARTLETT 1919, table 1)	flat	$\alpha\beta ff$	11		(See COBB and BARTLETT 1919, table 1)	flat	$\alpha\beta ff$	103	
×	×										
mut. *formosa*	$\alpha'\beta ff$		revolute mut.	$\alpha'\beta ff$	122			revolute mut.	$\alpha'\beta ff$	159	
mut. *formosa*	$\alpha'\beta ff$							flat	$\alpha'\beta FF$, $\alpha'\beta Ff$	5,337	2.70:1
×	×	11	flat	$\alpha'\beta Ff$	292		12				
f. *typica* M (homozygous)	$\alpha'\beta FF$							revolute	$\alpha'\beta ff$		
f. *typica* M (homozygous)	$\alpha'\beta FF$							flat	$\alpha'\beta FF$, $\alpha'\beta Ff$	4,300	2.65:1
×	×	13	flat	$\alpha'\beta Ff$	474		14				
mut. *formosa*	$\alpha'\beta ff$							revolute	$\alpha'\beta ff$		

mut. *formosa*	$\alpha'\beta ff$		flat	$\alpha'\beta Ff$				flat	$\alpha'\beta FF$		
×	×	15			59	0.85:1	16		$\alpha'\beta Ff$	1,849	2.69:1
f. *typica* M (heterozygous)	$\alpha'\beta Ff$		revolute	$\alpha'\beta ff$				revolute	$\alpha'\beta ff$		
f. *typica* M (heterozygous)	$\alpha'\beta Ff$		flat	$\alpha'\beta Ff$				flat	$\alpha'\beta FF$		
×	×	17			167	0.88:1	18		$\alpha'\beta Ff$	660	2.83:1
mut. *formosa*	$\alpha'\beta ff$		revolute	$\alpha'\beta ff$				revolute	$\alpha'\beta ff$		
f. *typica* E	$\alpha\beta ff$							flat	$\alpha\beta FF$		
									$\alpha\beta Ff$	6,089	
×	×	19	flat	$\alpha\beta Ff$	78		20		$\alpha\beta ff$		2.77:1
f. *typica* M (homozygous)	$\alpha'\beta FF$							revolute mut.	$\alpha'\beta ff$	0	
f. *typica* M (homoyzgous)	$\alpha'\beta FF$							flat	$\alpha'\beta FF$		
×	×	21	flat	$\alpha'\beta Ff$	694		22		$\alpha'\beta Ff$	2,299	
f. *typica* E	$\alpha\beta ff$							revolute	$\alpha'\beta ff$		
f. *typica* M (heterozygous)	$\alpha'\beta Ff$		flat	$\alpha'\beta Ff$				flat	$\alpha'\beta FF$		
×	×	23			174	0.89:1	24		$\alpha'\beta Ff$	701	3.24:1
f. *typica* E	$\alpha\beta ff$		revolute	$\alpha'\beta ff$				revolute	$\alpha'\beta ff$		
f. *typica* M (homozygous)	$\alpha'\beta FF$										
×	×	25	flat	$\alpha'\beta FF$	68		26	flat	$\alpha'\beta FF$	544	
f. *typica* C	$\alpha\beta FF$										
								flat	$\alpha'\beta FF$	4,671	
f. *typica* M (heterozygous)	$\alpha'\beta Ff$			$\alpha'\beta FF$							
×	×	27	flat		66		28	flat	$\alpha'\beta FF$		
f. *typica* C	$\alpha\beta FF$			$\alpha'\beta Ff$					$\alpha'\beta Ff$	3,374	3.50:1
								revolute	$\alpha'\beta ff$		

TABLE 30

Ratios of flat-leaved to revolute-leaved plants (given in terms of flat-leaved plants per thousand germinations) in all cultures in which the expectation is 750, assembled and classified according to percentage of germination.

Number of flat-leaved plants per thousand plants in each of the cultures of the accompanying tables in which the expected number is 750	PERCENTAGE OF GERMINATION										
	1–5	5–10	10–15	15–20	20–25	25–30	30–35	35–40	40–45	45–50	50–81
	627	476	611	681	635	652	667	708	702	718	736
	630	567	655	682	658	677	731	743	713	727	746
	639	606	678	704	678	720	745	751	729	742	772
	651	649	685	707	697	742	750	769	730		780
	652	667	712	711	717	745	799	808	739		838
	667	690	725	737	726	786	815	812			
	676	709	730	748	730	800					
	676	730	743	750	732						
	700	739	747	771	737						
	706	742	754	800	744						
	710	742	763		744						
	719	743	789		756						
	727	745	789		762						
	739	747	793		772						
	741	750	795		782						
	742	750	804		830						
	750	755	808		854						
	765	766	825		914						
	765	806	836								
	766	815									
	778	818									
	800	897									
	808	917									
	816										
	833										
	850										
	863										
	869										
	917										
Average...	744	732	750	729	748	732	751	765	726	729	774

GENETIC STUDIES ON *DROSOPHILA SIMULANS*. II. SEX-LINKED GROUP OF GENES[1]

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INTRODUCTION

It has been shown in Part I of these studies (STURTEVANT 1920 c) that *Drosophila simulans* may be hybridized with *D. melanogaster*, and that the hybrids are sterile. It had been hoped, had the hybrids been fertile, that the genetic make-up of *simulans* could be studied through the hybrids. This hope disappeared when the hybrids were found to be sterile, so the problem had to be attacked in another way,—namely, by studying the genetics of pure *simulans*. A number of mutations have been obtained, and it has been possible to show that certain of these are allelomorphs of known mutations of *melanogaster*. The genetic behavior of *simulans* is now fairly well worked out, and can be compared in some detail with that of *melanogaster*. The data concerning the sex chromosomes will be presented in this paper, and the autosomes will be discussed in Part III of these studies.

[1] Contribution from the CARNEGIE INSTITUTION OF WASHINGTON.

SEX-LINKED MUTATIONS OF *Drosophila simulans*

Table 1 shows the sex-linked mutations that have been found in *D. simulans*. A brief description of each and an account of its origin follows.

Yellow. The original specimen was collected on a pile of decaying tomatoes at Lakeland, Florida, by Dr. C. W. METZ. He obtained a stock from it and sent it to me before *simulans* had been recognized as a distinct species. This was one of the first stocks of *simulans* used in the experiments here reported.

The mutant character looks exactly like the yellow *melanogaster* that is already known, described and figured (MORGAN and BRIDGES 1916). We shall see below that it is in fact the same character.

TABLE 1

Sex-linked mutations of Drosophila simulans.

NAME	CHARACTER AFFECTED	SYMBOL	LOCUS	DATE	DISCOVERY BY WHOM	STOCK
Yellow	Body color	y	0.0	May, 1919	C. W. METZ	Wild, Fla.
Yellow	Body color	y	0.0	Oct. 15, 1919	A. H. S.	Wild, N. H.
Prune	Eye color	p_n	3.0	Aug. 29, 1919	A. H. S.	y l_b linkage
Dwarf	Size	d_w	3.0	Oct. 1, 1919	A. H. S.	y l_b linkage
Rubyoid	Eye color	r_d[2]	11.3	Oct. 31, 1919	A. H. S.	y p_n linkage
Carmine	Eye color	c_a[2]	44.8	Sept. 17, 1919	A. H. S.	y, scarlet
Forked	Bristles	f	57.2	Sept., 1919	C. B. BRIDGES	y stock
Tiny-bristle	Bristles	l_b[2]	57.8	July 8, 1919	A. H. S.	Wild, Fla.
Lethals	Life				A. H. S.	

[2] If these mutants were treated as though they were mutants of *D. melanogaster*, rubyoid would have the symbol rb^d, carmine would be g^e, and tiny-bristle would have to be renamed.

On October 15, 1919, I found a single yellow male in a wild stock from Randolph, New Hampshire. This male was bred to wild-type females, and in F_2 there appeared many yellow males. One of these was crossed to a female known to be heterozygous for the original Florida yellow, and produced many yellow daughters. Since the two yellows were indistinguishable, and were shown by this experiment to be allelomorphic, the New Hampshire yellow was discarded. It was used in none of the linkage experiments recorded in this paper. It is possible that this race arose by contamination with the Florida yellow, rather than by mutation, as no conclusive check against such an accident was available.

Prune. A single male with a dark purplish translucent eye was found on August 29, 1919, in a culture of pure Florida ancestry (two females were used in making up this culture), that produced 81 other males, all with the usual red eye-color. A stock was obtained from this male, and

has been used extensively in the experiments here recorded. The eye-color looks almost exactly like the prune eye-color of *melanogaster*, and is in fact due to a mutation in the same locus, as we shall see later.

Dwarf. Culture 6883, from a single female heterozygous for yellow, counted in October 1919, produced 74 ♀♀, 3 not-yellow ♂♂, 27 yellow ♂♂. The family was continued as a lethal strain, and gave results consistent with the view that there was a sex-linked lethal present, which was very close to prune. Later it was noticed that the apparent crossovers between prune and the lethal were all dwarfs. These dwarfs proved fertile, and it has been shown by breeding them that they actually carry the supposed lethal. The lethal (really semi-lethal) effect and the dwarf character are evidently due to the same gene, which is conveniently referred to as "dwarf," rather than "lethal," the original name.

Rubyoid. Culture 7108, of pure Florida ancestry, contained a single female, that carried one yellow prune X while the other X was supposed to be wild-type. At least 38 sons (33 of them not yellow) had a new eye-color, much paler than prune. The female in 7108 evidently had in her "wild-type" (maternal) X a new mutation. The mother of this female produced no rubyoid sons, nor did 9 tested sisters of 7108, though at least five of these probably carried the same maternal X (so far as the left-hand end was concerned) as did 7108. The situation is, however, somewhat obscured by the fact that the mother of 7108 and some of her sisters were heterozygous for dwarf, which acted practically as a lethal; and also by the possible presence of a second lethal in the same general region.

The color of the rubyoid eye is somewhat darker than that of ruby *melanogaster*, with which it is allelomorphic, but is of the same general nature.

Carmine. This eye-color appeared first in a single male, from a culture made up with two females, both heterozygous both for yellow and for the autosomal recessive scarlet. The original mutant male was also yellow. The culture from which he came was of pure Florida stock, and was a daughter culture of 6701, in which prune first appeared.

Carmine closely resembles the *melanogaster* mutant of the same name. As we shall see, both are allelomorphic to the more familiar garnet of *melanogaster*. The eye-color is paler than that of rubyoid.

Forked. This mutant was discovered by Dr. C. B. BRIDGES in September 1919, in a stock of the Florida yellow. BRIDGES found that it was sex-linked, and that it gave free crossing over with yellow. The data on its linkage presented here, however, are all from my own experiments, made with a stock obtained from BRIDGES.

The character is exactly like the forked of *melanogaster*, which has been described and figured by MORGAN and BRIDGES 1916). The two characters are due to mutations in the same locus, as will appear below.

Tiny-bristle. A single female, of the Florida stock, was found to have an extra dorsocentral bristle. This character reappeared in only one of her descendants; but 38 of her 66 sons had small bristles. The small-bristle character is a sex-linked recessive in inheritance. There are several other effects associated with it. The flies hatch somewhat later than their normal brothers and sisters, and are more easily killed, as larvae or pupae, by unfavorable conditions. All the females so far tested have been completely sterile. In addition the eyes are often slightly roughened, and may have a slight nick in the anterior margin, and the abdominal bands are less pigmented than in wild-type flies and may be somewhat irregular.

Lethals. At least two lethals, besides the semi-lethal dwarf, have been found. Both were near the yellow locus, and were therefore not favorable for studying crossing-over relations, since this region is sufficiently well workable through yellow, prune and rubyoid. These lethals were therefore discarded, and it seems not worth while to present here what few data were obtained concerning them.

PARALLELISM OF SEX-LINKED MUTATIONS IN *simulans* AND *melanogaster*

The seven sex-linked characters described above all resemble sex-linked characters already known in *D. melanogaster*. Since the two species can be crossed, with the production of wild-type females, it is possible to find out if the mutant genes in the two species are allelomorphic. If a wild-type individual of either species is crossed to an individual of the other species that carries a recessive mutant gene, the daughters (except the one non-disjunctional exception referred to in Part I) are always wild-type in appearance, just as they are when a similar cross is made within either species. That is, each species carries the dominant normal allelomorphs of all the recessive mutant genes of the other species that have been tested. If, then, we cross a mutant race, say yellow, of *simulans* to a yellow race of *melanogaster*, we can determine whether or not the mutations have affected the same wild-type allelomorph, i.e., whether or not they are themselves allelomorphic. For clearly, if the hybrid females are not yellow, each parent has introduced the normal allelomorph of the mutant gene present in the other race, and the mutant genes are not allelomorphic. But if the hybrid females are yellow, then neither parent carried the normal

allelomorph of the yellow gene present in the other parent; and, since the wild-type flies do carry such allelomorphs wherever the test has been made, it follows that the two mutant yellows must be allelomorphs. We may now consider the data that have been obtained in experiments designed to test the allelomorphism of the seven sex-linked mutants of *D. simulans*.

Yellow

Eleven females from a stock of *melanogaster* pure for yellow and for white were mated to 19 yellow *simulans* males. Ninety-three yellow white females (*melanogaster*, and due to non-virginity of the mothers), 117 yellow white males (also *melanogaster* and due to non-virginity), and 41 yellow females (hybrid, and not white) were produced. The 41 yellow females that were not white prove that the two yellows are allelomorphic.

Prune

Seven *melanogaster* females from a stock pure for yellow and for prune were mated to six *simulans* males that were prune (not yellow). Thirty offspring were produced—all of them prune (not yellow) females, thus proving the mutant genes to be allelomorphic.

Dwarf

Hybrids have not been obtained in the case of the two dwarfs, and in *simulans* the mutant has been lost, so that we can get only indirect evidence here.

In both species the dwarf gene is a semi-lethal, and in both the dwarf males appear normal except for their small size and the pale color that is usually associated with small size arising from any cause (such as starvation of the larva) in Drosophila. The dwarf males are fertile in both species; in *simulans* the few females that have been tested have proved sterile. In *simulans* dwarf has not been found to cross over from prune (except in one doubtful instance) and accordingly has a locus of 3.0; in *melanogaster* I have reared many flies without getting a crossover between dwarf (known in this species as "lethal 10") and either yellow or scute, which are both located at 0.0. Dwarf prune crossovers in *melanogaster* have however been found on two occasions. Dwarf thus sticks closely to prune in *simulans*, and to yellow in *melanogaster*. The yellow prune crossover value is 1.1 in *melanogaster*, 3.0 in *simulans*. It seems probable that the two dwarfs are not identical, in spite of their similarity and the nearness of their loci, and that this case is similar to that of the two tiny-bristles discussed below. However, it

is possible that the dwarf locus is between the yellow and prune loci, and that the yellow prune crossing over in *melanogaster* is all or nearly all to the right of this locus, while in *simulans* it is all or nearly all to the left of it. This view is rendered improbable by a consideration of the crossover relations of rubyoid *simulans* and ruby *melanogaster*, to be discussed later. If the one doubtful prune dwarf crossover in *simulans* is really a crossover, he indicates that dwarf is to the right of prune, thus again negativing the above tentative interpretation; but as will appear below his nature is very doubtful.

Rubyoid

Nine *melanogaster* females from a stock pure for ruby were mated to 13 rubyoid *simulans* males. The offspring were 224 in number, all of them females with an eye-color intermediate between ruby and rubyoid. The two mutant genes are thus allelomorphs.

Carmine

Two *melanogaster* females from a stock pure for vermilion, garnet, small, and forked were mated to four carmine *simulans* males. The offspring consisted of 32 females, all with an eye-color intermediate between carmine and garnet. Since the mother had two eye-color mutations (vermilion and garnet), this case is not quite as certain as the others here described. But vermilion is a very different-looking color from the other two, which are quite similar; and carmine is almost exactly like the mutant of the same name known in *melanogaster*, which is an allelomorph of garnet. These facts, taken in connection with the observation that the eyes of the 32 hybrids did not look at all like vermilion, but were intermediate between carmine and garnet, leave no reasonable doubt that carmine *simulans* is an allelomorph of garnet *melanogaster*.

Forked

A *melanogaster* female from a stock pure for eosin, vermilion, and forked was mated to a forked *simulans* male. Forty-nine offspring were produced, all of them forked daughters. The two mutant genes are therefore allelomorphs.

Tiny-bristle

The tiny-bristle females are sterile in both species, so in this case it was necessary to use *melanogaster* females heterozygous for tiny-bristle. Two

tests were made. In the first case six females of the constitution[3] $\frac{v\,f}{t_b}$ were mated to 21 tiny-bristle *simulans* males. The following offspring resulted:

FEMALE			MALE			
Wild-type	*v*	*vf*	t_b	*vf*	*v*	t_b
99	78	26	10	14	11	19

The mothers were evidently not all virgin, since sons (and pure *melanogaster* sons) were produced. At least one of the females had mated with a vermilion forked *melanogaster* male, but the excess of females, especially in the wild-type class, indicates that some of the offspring were actually hybrids. Since the cross was not conclusive another test was made. Seven *melanogaster* females of the same constitution as before were mated to 12 tiny-bristle *simulans* males. The offspring are shown below:

FEMALE				MALE		
Wild-type	*v*	*vf*	*f*	t_b	*vf*	*v*
133	4	5	1	5	3	2

Though here again at least one of the mothers was not virgin, the very great excess of females leaves no doubt that most of the offspring were hybrids. And, as in the previous test, *no tiny-bristle daughters appeared*. The two mutant genes thus are not allelomorphic, though their effects correspond in detail, and are more numerous than those of most mutant genes.

MAP OF THE *simulans* X CHROMOSOME

All experiments designed to test the linkage between the sex-linked genes of *D. simulans* are summarized in tables 2, 3, and 4. The totals for each type of cross are given separately, but it has not seemed worth while to publish the counts for each individual culture.

Table 5 shows the total data for each pair of loci.

These data, more especially the three- and four-point data (tables 3 and 4), show clearly that the sequence of the genes is yellow, prune, rubyoid, carmine, forked, tiny-bristle. Dwarf is close to prune, and its position has already been discussed.

[3] *v* = vermilion, t_b = tiny-bristle, *f* = forked.

TABLE 2

Two-point linkage experiments with the X chromosome of D. simulans.

LOCI	TYPE OF CROSS	NON-CROSSOVERS		CROSSOVERS		TOTAL
y p_n	*y p_n* × +	1504	1438	39	50	3031
	y × *p_n*	395	427	18	8	848
y r_d	*y r_d* × +	114	130	6	11	261
	y × *r_d*	98	103	15	15	231
y c_a	*y c_a* × +	1120	951	514	461	3046
	y × *c_a*	80	111	69	57	317
y f	*y f* × +	173	191	116	117	597
y l_b	*y l_b* × +	493	190	162	410	1255
	y × *l_b*	296	347	311	221	1175
p_n r_d	*p_n* × *r_d*		66	8		74
p_n c_a	*p_n* × *c_a*		181	78		259
p_n l_b	*p_n* × *l_b*	12	97	75	17	201
d_w r_d	*d_w* × *r_d*	359	45	48	0	452
r_d c_a	*r_d* × *c_a*			12		90
r_d f	*r_d* × *f*	47	51	19	28	145
r_d l_b	*r_d* × *l_b*	78	160	87	21	346
c_a f	*c_a* × *f*	71	82	5	5	163
c_a l_b	*c_a* × *l_b*	42	95	21	7	165

NOTE. In tables 2, 3 and 4, the column headed "Loci" shows not only the loci concerned, but also their sequence. In the third and following columns classes are entered under their headings indicating the type of crossing over they represent. In every case that class which includes the individuals bearing the dominant (wild-type) allelomorphs in the left-hand locus concerned is placed first, and is followed by the contrary class.

TABLE 3

Three-point linkage experiments with the X chromosome of D. simulans.

LOCI	NATURE OF CROSS	NON-CROSSOVERS		SINGLE CROSSOVERS				DOUBLE CROSSOVERS		TOTAL
				Region 1		Region 2				
y p_n d_w	*y p_n* × *d_w*	58	501	18	0	0	1[4]	0	0	578
y p_n f	*y p_n* × *f*	130	127	3	0	65	73	1	0	399
y p_n l_b	*y p_n l_b* × +	68	30	0	0	26	48	0	0	172
	y p_n × *l_b*	49	109	3	8	98	35	1	2	305
	y × *p_n l_b*	27	54	3	0	25	9	0	1	119
	y l_b × *p_n*	77	21	2	7	13	52	4	0	176
y r_d c_a	*y c_a* × *r_d*						25	5		284
y r_d f	*y* × *r_d f*	86	91	10	11	33	34	2	1	268
	y f × *r_d*	391	355	56	46	180	200	23	11	1262
y r_d l_b	*y r_d l_b* × +	14	10	4	2	4	8	1	1	44
	y r_d × *l_b*	3	33	3	0	15	5	1	1	61
	y l_b × *r_d*	126	36	9	30	25	102	16	4	348
y c_a f	*y c_a* × *f*	725	719	419	383	134	109	34	32	2555
y c_a l_b	*y c_a l_b* × +.	167	29	54	110	16	45	19	8	488
	y c_a × *l_b*	38	61	49	27	10	9	1	13	208
	y l_b × *c_a*	56	35	24	46	14	6	6	7	194
r_d c_a f	*r_d* × *c_a f*			58				8		349
r_d f l_b	*r_d l_b* × *f*	84	20	23	23	0	0	0	1	151

[4] This individual was yellow prune dwarf in appearance; but frayed was later found to be in the stock, and may have been responsible for his small size. He was sterile.

In constructing the map, the yellow prune, yellow rubyoid, carmine forked, and forked tiny-bristle values of table 5 have been used directly. These are based on large enough numbers to be reasonably accurate, and the distances are all short enough so that possible double crossovers must be so rare as to be negligible.

TABLE 4

Four-point linkage experiments with the X chromosome of D. simulans.

LOCI	NATURE OF CROSS	NON-CROSS-OVERS		SINGLE CROSSOVERS						DOUBLE CROSSOVERS						TRIPLE CROSS-OVERS		TOTAL
				Region 1		Region 2		Region 3		1, 2		1, 3		2, 3				
$y\ r_d\ f\ l_b$	$y\ r_d\ f\ l_b \times +$	54	23	2	10	21	57	1	0	5	3	0	0	0	0	0	0	176
$y\ c_a\ f\ l_b$	$y\ c_a\ f \times l_b$	99	126	95	69	25	23	1	1	9	11	1	1	0	0	0	0	461
	$y\ c_a\ l_b \times f$	398	193	169	311	51	65	0	3	34	15	4	0	0	0	0	0	1243
	$y \times c_a\ f\ l_b$	39	107	69	28	12	10	1	0	2	8	0	0	0	0	0	0	276

TABLE 5

Total data for each pair of loci in the X chromosome of D. simulans.

LOCI	TOTAL	CROSSOVERS	PERCENTAGE OF CROSSING OVER
$y\ p_n$	5628	168	3.0
$y\ d_w$	578	19	3.3
$y\ r_d$	2651	299	11.3
$y\ c_a$	9064	3266	36.0
$y\ f$	7513	3131	41.6
$y\ l_b$	6977	3194	45.8
$p_n\ d_w$	578	1	0.2
$p_n\ r_d$	74	8	10.8
$p_n\ c_a$	259	78	30.1
$p_n\ f$	399	139	34.8
$p_n\ l_b$	973	406	41.7
$d_w\ r_d$	452	48	10.6
$r_d\ c_a$	723	108×2	29.9
$r_d\ f$	2002	664	33.1
$r_d\ l_b$	1126	424	37.6
$c_a\ f$	4974	616	12.4
$c_a\ l_b$	3311	492	14.9
$f\ l_b$	2583	15	0.6

The rubyoid carmine value, which is necessary in the construction of the map, is not so easily determined. The direct method, of crossing the two mutants and determining the amount of crossing over between them, is not entirely satisfactory, because rubyoid and carmine cannot be distinguished from each other or from the double recessive, rubyoid carmine, with any degree of certainty. All three are, however, easily distinguishable from the wild-type. Several counts from females with rubyoid in one X

and carmine in the other are recorded in table 5. Since the wild-type flies constitute one-half of the total number of crossovers, we may calculate the crossover percentage by doubling this number and dividing it by the whole number of offspring. This method indicates a crossover percentage of 29.9.

The value just obtained is open to some question, since it is based on rather small numbers and since it would be seriously affected by viability complications, owing to the fact that only one of the crossover classes was distinguishable. Accordingly two other methods of calculating the value have been carried out. The first of these consists in using the well-established yellow carmine value, 36.0, corrected for observed yellow rubyoid carmine double crossing over (3.5 percent, which must be doubled and added to 36.0 for our purpose). The resulting value, 43.0, minus the observed yellow rubyoid value of 11.3, gives a second rubyoid carmine value, 31.7.

TABLE 6

Coincidence in the X chromosome of D. simulans.

LOCI	TOTAL FLIES	NUMBER OF DOUBLE CROSSOVERS	PERCENTAGE OF CROSSOVERS, REGION 1 + REGION 2	COINCIDENCE
y p_n d_w	578	0	3.3	
y p_n *f*	399	1	35.8	50
y p_n l_b	772	8	45.2	72
y r_d *f*	1706	45	43.9	74
y r_d l_b	629	32	57.5	81
y c_a *f*	4535	145	50.1	68
y c_a l_b	2870	139	56.4	77
r_d *f* l_b	327	1	41.2	127

NOTE. The first three experiments and the last one showed such small numbers of double crossovers that the coincidence values are not significant. They have been included here only for the sake of completeness.

The third method of calculation is based on the well-established rubyoid forked value, 33.1. Corrected for observed rubyoid carmine forked double crossing over (4.6, which must be doubled), this value becomes 42.3. Subtracting the observed carmine forked value of 12.4 gives 29.9 as a third value for rubyoid carmine. The three values, 29.9, 31.7, and 29.9, show quite as close an agreement as was to have been expected. The average of the three, 30.5, has been used in constructing the map.

There is, however, another difficulty here. The value 30.5 corresponds to a distance long enough so that double crossing over must be supposed to occur within it. There is no method of ascertaining how much to allow for such double crossing over, until mutations in the region are discovered

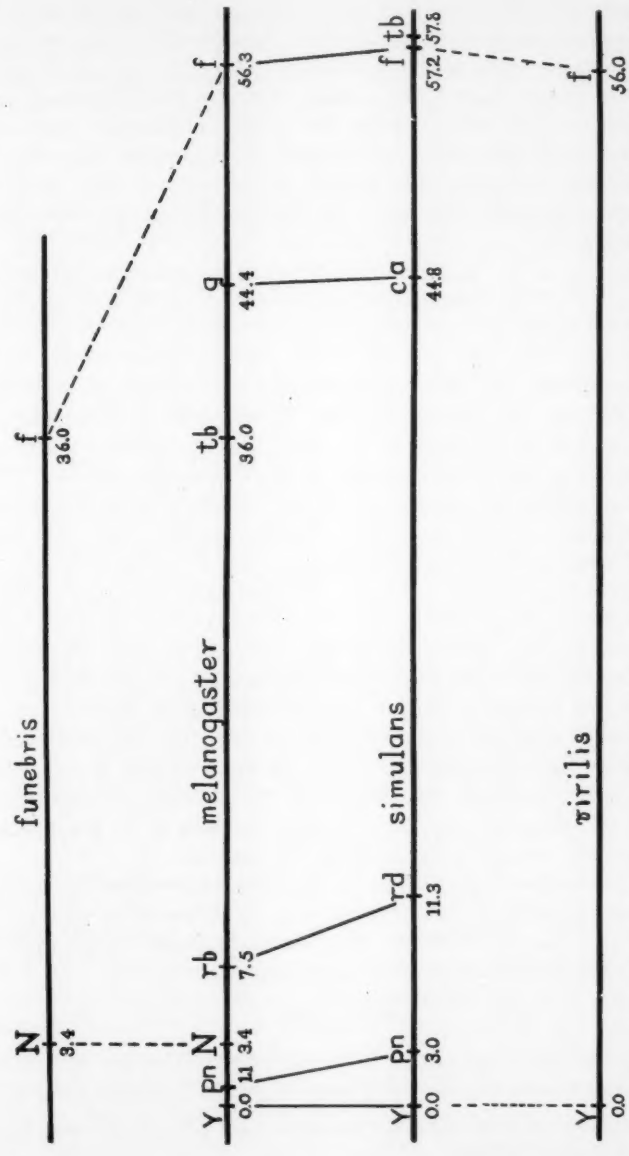

FIGURE 1.—Maps of the X chromosomes of four species of Drosophila. The dotted lines connect genes that are inferred to be allelomorphic because of the similarity of the characters concerned; the solid vertical lines connect genes that have been definitely shown to be allelomorphic.

and studied. However, we shall see in the following section that the double-crossing-over relations in the X of *simulans* that can be studied, are very similar to those of the X of *melanogaster*. Accordingly it seems legitimate to correct the rubyoid carmine value by the addition of three units, which is about the correction that would be necessary for a like value in the X of *melanogaster*. The value 33.5 has therefore been adopted as corresponding to the "distance" between the two loci. It must, however, be emphasized that later work may show that this value requires changing by a few units.

The resulting map, together with a map of the corresponding loci of *D. melanogaster* (chiefly from extensive data collected by Dr. C. B. BRIDGES and in part unpublished) (compare BRIDGES 1919 for some of the loci), is shown in figure 1.[5] This map shows that the sequence of the five corresponding loci in the two species is the same, but that the amount of crossing over is not the same. In the left-hand end of the chromosome there is more crossing over in *simulans*, in the middle there is probably somewhat less, while in the right-hand end there is about the same amount. This difference in amount of crossing over is not surprising, since it has been shown (BRIDGES 1915, PLOUGH 1917, STURTEVANT 1919, etc.) that the amount of crossing over is not constant even within the same species. I have shown in the paper referred to that genetic factors may cause changes, even greater than those here described, in the second chromosome of *D. melanogaster;* and also that such changes, as in the present case, do not always affect different parts of the same chromosome proportionately.

The previous studies on linkage variations within one species have all shown that the sequence of the loci is not altered by such variations as occur. That the present example shows the same relation is important, for it indicates that the X chromosomes of the two distinct species have essentially the same constitution. Not only are many of the genes identical, but they are arranged in the same relative positions.

The map corroborates the conclusion that the "tiny-bristles" in the two species represent different mutations, for their respective loci are on opposite sides of the garnet-carmine locus. This fact was not discovered until the negative test of allelomorphism had been completed.

COINCIDENCE

Table 6 shows the total available three-point data that can be used for calculation of coincidence, including those which can be extracted from the

[5] See the appendix of this paper for a discussion of the maps of the *virilis* and *funebris* X chromosomes, also shown in the figure.

four-point crosses. The coincidence values are close to those that have been observed for similar distances in *melanogaster*, but perhaps average a little lower. Detailed comparison is not easily made from the available data, and will not be attempted here.

NON-DISJUNCTION

Non-disjunction of the sex chromosomes occurs in *D. simulans*, and in the same way as in *D. melanogaster* (see BRIDGES 1916), so far as it has been investigated.

It has been shown, by the use of the mutant character scarlet, that the third chromosome pair is distributed as usual in females that are producing non-disjunctional exceptions.

Exceptional females have been found to produce further exceptions. Seventeen tests of exceptional yellow females, mated to not-yellow males, have given a total of 1079 not-yellow daughters, 1062 yellow sons, 39 yellow daughters, and 26 not-yellow sons. The percentage of secondary exceptions calculated from these data, 2.9, is somewhat less than the percentage (4.3) found by BRIDGES to be normal for *D. melanogaster;* but the difference is probably not significant, for in both species the percentage is a quite variable quantity.

In *D. simulans*, as in *melanogaster*, some of the regular daughters of an exceptional female produce exceptions, while others do not. No cytological examination has been made of XXY *simulans*, and the sterility of the XO males has not been adequately tested.

In general, the two species behave very similarly with respect to non-disjunction, and we may safely conclude that the mechanism demonstrated by BRIDGES for *melanogaster* is the one that is at work in *simulans*.

GYNANDROMORPHS

Seven gynandromorphs have been found in *D. simulans*. The general conclusions to be deduced from a study of them are in agreement with those reached by MORGAN and BRIDGES (1919) as a result of their examination of a large series of gynandromorphs obtained in *D. melanogaster*. Nevertheless it seems worth while to put on record the data obtained with *simulans*.

The first gynandromorph was obtained, December 13, 1919, from a mating of a female, with yellow and rubyoid in one X and tiny-bristle in the other, by two rubyoid males. This female and at least one of the males were heterozygous for the autosomal recessive eye-color scarlet.

The daughters from this mating were 46 wild-type, 47 rubyoid (disregarding scarlet) and the gynandromorph that is shown in figures 2 and 3. This specimen was a wild-type female in all respects except that the right eye was partly rubyoid, and some of the head-bristles were smaller than their mates and were therefore probably male. The left eye was wild-type, there were no sex-combs, and the individual bred as a female. Mated to scarlet males it produced 21 wild-type daughters, 20 scarlet daughters, 8 wild-type (and scarlet) sons, and 18 rubyoid (and rubyoid scarlet) sons. The female parts of the gynandromorph thus had one rubyoid (paternal) X and one wild-type X that was due to a crossover in the mother, between rubyoid and tiny-bristle. The maternal X was eliminated from a cell that gave rise to part of the right side of the head.

FIGURE 2

FIGURE 3

FIGURES 2 and 3.—The first gynandromorph discovered in *Drosophila simulans*.

The second gynandromorph appeared, January 17, 1920, in a mating of two yellow females by two wild-type males. The specimen was wild-type female on the right side (no sex-comb, longer wing, female abdominal pattern), and yellow male on the left side (sex-comb, shorter wing, male abdominal pattern). The genitalia, however, were entirely yellow and male. On the right side there was a narrow wild-type-colored sixth dorsal abdominal tergite, and the right half of a fifth ventral plate[6] (also wild-type in color), behind which were the male genitalia, normal in structure but yellow in color. The incomplete sixth dorsal tergite did not fuse with the fifth of the left side, but narrowed to a point near the mid-dorsal line. The internal genitalia were male, including two small pale testes.

The gynandromorph probably resulted from the elimination of a paternal X at an early division.

[6] Normal males have only five dorsal and four ventral abdominal plates aside from the genital segments; females have seven dorsal and six ventral ones (see figures in Part III of these studies). The fifth dorsal plate of the male bears two pairs of spiracles, and evidently represents two fused plates, i.e., it is homologous to both the fifth and the sixth of the female.

The third gynandromorph appeared, February 10, 1920, in a culture produced by a female with yellow and prune in one X and forked in the other, mated to three yellow prune males. The specimen was wild-type and female on the right side of the head and thorax (no sex-comb, longer wing) and in most of the abdomen. The male parts were yellow (neither prune nor forked), and included the left side of the head and thorax (sex-comb, shorter wing), and part of the abdomen. The external genitalia (ovipositor plate and anal plate) on the right side were wild-type and female, and on this side there were the six dorsal tergites of the normal female. On the left side there were only five dorsal tergites, and then followed *two* distinct male first genital tergites, both yellow in color. No anal plates were observed on this side. The presence of two male parts and one female in the external genitalia is distinctly unusual among gynandromorphs; and this specimen was also unusual in other ways. Dr. J. F. NONIDEZ dissected it, and made the drawing here reproduced (figure 4). The uterus and receptacles were normal female organs, but were connected with small testes in which Dr. NONIDEZ observed active sperm. The small bodies attached below the testes are of uncertain nature, though Dr. NONIDEZ states that they looked superficially more like ovaries than like the usual accessory glands of the male. They were, however, not studied in detail.

FIGURE 4.—Internal genitalia of the third gynandromorph. Dissection and drawing by Dr. J. F. NONIDEZ.

The origin of this gynandromorph presents certain difficulties. Since its father was yellow prune, but the female parts were not yellow or prune, the maternal X must have been either wild-type or forked. Furthermore, this maternal X must have been the one eliminated,—yet the male parts included an eye that was not prune, though the paternal X certainly carried prune. It seems probable that the gynandromorph received *two* maternal X's, one yellow and not prune or forked (a double crossover), and one either wild-type or forked. These X's may have been in the same nucleus, causing an XXX zygote; or, what seems more likely, they may have been in separate nuclei and fertilized by separate sperm. These two possible origins have been discussed at some length by MORGAN and BRIDGES (1919), so will not be gone into here. The fact that this gynandromorph showed extra parts in the external genitalia (and perhaps also in the gonads) may perhaps be taken as arguing for the double-nucleus origin, but is certainly not conclusive.

Another possible interpretation of this gynandromorph is based on the assumption that prune, like vermilion in *melanogaster* (STURTEVANT 1920 b), is not self-differentiating. If the color of a prune eye is determined, not by the genetic constitution of the eye pigment itself, but by that of some other portion of the body, then the present gynandromorph may be explained very simply, as being due to the elimination of a maternal X at an early division.

The fourth gynandromorph appeared, March 17, 1920, in a culture produced by a female heterozygous for yellow and for the autosomal recessive eye-color plum, mated to a plum male. The gynandromorph (figure 5) was anteriorly largely wild-type and female, but was yellow and male in part of the thorax and most of the abdomen. The head and legs were entirely wild-type and female (no sex-combs). The right side of the thorax was entirely wild-type and female, and the right wing was distinctly larger than the left. There was a streak of yellow on the left side including the left acrostical hairs, dorsocentrals, scutellars, postalars, presutural, and the posterior supraalar, but not the other thoracic bristles of the left side. The left wing was wild-type anteriorly, yellow posteriorly. Apically the dividing line, as shown in the figure, was clearly just anterior to the third vein. Basally the division was difficult to determine: the two branches of the dotted line in the figure show its possible limits, the region between the branches being impossible to identify either as wild-type or as yellow. It does not follow that this region was intermediate in character, as the differences to be seen in this region between wholly yellow and wholly wild-type wings are slight. The whole wing, though it included a female anterior margin, was approximately of the size characteristic of males. The abdomen was yellow and male, except for the right half of the first dorsal tergite, which was wild-type and female. The individual was found to be sterile as a male. It can easily be accounted for by the elimination of a paternal X at an early division.

The fifth gynandromorph appeared, March 20, 1920, in culture 8362. The mother was heterozygous for yellow, and both parents were heterozygous for the second-chromosome recessive mutant genes plum and intersex. There were no traces of these autosomal characters in the gynandromorph, but the intersex character (see STURTEVANT 1920 a, and Part III of these studies) could have been detected only had genitalia been present on the female parts, which was not the case. The gynandromorph was wild-type and female on the left side, yellow and male on the right, throughout the body except the external genitalia. These were yellow and male on both sides. No spermathecae were present, and gonads

were not found on hasty dissection. The gynandromorph evidently arose through the elimination of a paternal X at an early division.

The sixth and seventh gynandromorphs were produced, April 1920, by the same culture, which was made up by mating two scarlet (autosomal recessive) females to three not-scarlet males. At least one of these males was heterozygous for scarlet. No sex-linked mutant genes were present, so that no analysis of the origin of the gynandromorphs is possible.

FIGURE 5.—The fourth gynandromorph. The dotted line on the left wing marks the division between the yellow and not-yellow portions.

Number six (found April 5) showed no trace of scarlet. The head, most of the thorax, both front tarsi, and the left wing were female. The right wing was male. The abdomen was female-colored on the right side, male-colored on the left. There were five dorsal abdominal tergites on each side; on the right side the fifth one was narrow and had one spiracle, on the left it was broad and had two spiracles,—the normal sexual difference. There were four ventral abdominal plates, with two more half-plates on the female side, these being behind and displaced toward the right side of the body. The external genitalia were male, and were twisted around so that the dorsal line of the first genital tergite was opposite the lower

edge of the fifth dorsal tergite on the left side. A penis, two testes, and two male accessory glands were present; there were no ovaries or receptacles.

Number seven (found April 7) was female anteriorly, with no sex-combs, and had a female right wing. The left wing was male, as was the abdomen, including testes and accessory glands. This specimen had scarlet eyes.

As stated above, these gynandromorphs do not add materially to the conclusions derived by MORGAN and BRIDGES from their study of gynandromorphs of *D. melanogaster*. They serve to bring out again the fundamental similarity of the genetic processes occurring in the two species. Aside from this their chief interest lies in two specimens,—number three, which represents a new example of one or the other of two rare types of gynandromorphs, and was unusual in having three sets of external genitalia instead of the usual two; and number four, which is the only Drosophila gynandromorph known to me that has a wing that is a mosaic of male and female parts. This last specimen is interesting in that the mosaic wing was male in size, instead of being intermediate or of abnormal shape. It indicates that the length of the anterior margin of the wing is not self-differentiating, but depends upon other factors,—presumably upon the nature of the rest of the wing.

ABSENCE OF GYNANDROMORPHS AMONG THE *melanogaster-simulans* HYBRIDS

It seemed not unlikely that irregularities in cell-division might be more frequent in the *melanogaster-simulans* hybrids than in either pure species, since it is known that irregular distribution of the chromosomes does occur in many species hybrids. One type of irregularity,—viz., the elimination of an X chromosome at an early division,—occurs rarely in both species and gives rise to gynandromorphs. MORGAN and BRIDGES (1919) have shown that in *melanogaster* such elimination occurs, and causes gynandromorphs that can be detected, in about one out of each 1100 eggs fertilized by X-bearing sperm.

I have examined a few more than 1300 hybrid females, and have carefully scrutinized each one with this point in mind, but have found no gynandromorphs at all. Over 400 of these hybrids were heterozygous for yellow, a circumstance that makes the detection of gynandromorphs especially easy. Many of the others were heterozygous for other sex-linked genes that would also increase the likelihood of detection, though to a less extent. We may conclude that gynandromorphs are at most not much more frequent among the hybrids than in pure *melanogaster*. This constitutes still further evidence that the two species have essentially similar germ-plasms.

SOMATIC MUTATIONS

On two occasions variations have appeared in single individuals of *D. simulans* that were to all appearances mutations, but that were not inherited. They were probably due to mutation in the somatic tissue of the individuals that showed the new characters. The germ-cells had evidently not undergone mutation.

Culture 7863 contained two yellow carmine scarlet females (of which one at least was XXY) and three scarlet males. There were 32 sons, of which two were scarlet (due to non-disjunction), and the remaining 30 were yellow carmine scarlet as expected. The carmine scarlet eye is a clear yellow in color; but one of these males had eyes that at first appeared to be white. Closer examination showed small patches of yellow color, and also showed that the ommatidia were enlarged and somewhat flattened. Dr. C. B. BRIDGES, who examined the specimen, pronounced it intermediate between "lozenge" and "lozenge 2," allelomorphic sex-linked mutants of *D. melanogaser*. This male was mated to two forked females, of an unrelated stock. Seventy-eight daughters and 80 sons were produced, one of the sons being a non-disjunctional exception. None of these showed any trace of the unusual character of their father's eye. The non-disjunctional son, since he had a paternal X, showed either that the mutant gene was not sex-linked, or that not all (and therefore probably not any) of the germ-cells of the mutant male carried it. This latter conclusion was borne out by the fact that seven daughters of the mutant male were tested, two of them by mating to their brothers, and all failed to produce lozenge-like offspring. It follows that even if the mutation was not sex-linked, it was not inherited.

FIGURE 6.—Left eye of somatic mosaic from culture 8368. The drawing was made after the specimen was dead, and most of the hairs and bristles had been rubbed off.

Culture 8368 was made by mating a female with yellow and carmine in one X and forked in the other, to four yellow carmine tiny-bristle males. Among the 115 sons of the expected classes was one that was yellow forked, and had a wild-type right eye. The left eye (figure 6) was a mosaic of the wild-type color and white. This male was mated to three females of a wild-type stock, and produced 53 wild-type offspring. Five females from this last culture were mated individually to brothers, and produced from 35 to 116 offspring each. These included the expected classes with respect to yellow and forked, but all had wild-type eyes. The white color present in the original male was therefore not inherited.

In both the cases just described it is possible that we are dealing not with mutations but with accidents of development, due perhaps to injury. The nature of the characters concerned, and their resemblance to known mutant characters of *melanogaster*, makes it more probable that they are examples of somatic mutation.

SUMMARY

1. Seven sex-linked mutants of *Drosophila simulans* are described. All strongly resemble known sex-linked mutants of *D. melanogaster*.

2. Six of these have been tested for allelomorphism with the corresponding *melanogaster* types, by crosses.

3. Yellow, prune, rubyoid, carmine, and forked *simulans* are shown to be allelomorphic to yellow, prune, ruby, garnet, and forked *melanogaster*, respectively.

4. Tiny-bristle *simulans* is not allelomorphic to tiny-bristle *melanogaster*, though strikingly similar to it.

5. A map of the *simulans* X chromosome is based on the crossing-over relations of these sex-linked mutations.

6. The sequence of the five allelomorphic mutations in *simulans* and *melanogaster* is the same in the two species, but the amount of crossing over is not identical.

7. The coincidence values for the two species are similar.

8. Non-disjunction occurs in *simulans*. The percentage of secondary exceptions observed was 2.9.

9. Seven gynandromorphs are described. These fit in with the conclusions reached through studies on *melanogaster* gynandromorphs.

10. Gynandromorphs are at most not significantly more frequent among the *melanogaster-simulans* hybrids than in pure *melanogaster*.

11. Two somatic mutations in *simulans* are described. Each resembled a known mutation of *melanogaster*, and neither was inherited.

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APPENDIX—X-CHROMOSOME MAPS OF *virilis* AND *funebris*

METZ (1918) has published data on the sex-linked mutant genes of *Drosophila virilis* Sturtevant. Two of the mutant characters, yellow and forked, appear very similar to the characters of the same names in *melanogaster* and *simulans*. Since *virilis*, which is a very distinct species, cannot be crossed to either of these, it is not certain that we are here dealing with identical loci. However, there is much evidence that strongly suggests such to be the case. The characters are closely similar in the three species; the evidence from *melanogaster* and *simulans* shows that in those species the two loci are relatively highly mutable, so that they might be expected to mutate also in a third species; and the positions occupied by the two loci in the *virilis* map are about the same as those established in *melanogaster* and *simulans*. The data presented by METZ indicate that the yellow-forked distance is about 56,—a strikingly close approximation to the values (56.3 and 57.8) obtained for the other two species.

I have published elsewhere (STURTEVANT 1918) an account of notch, a parallel mutation in *D. funebris* Fabricius. As was pointed out in that paper, notch *funebris* and notch *melanogaster* are alike in so many respects that there can be little doubt that they are allelomorphs, even though the two species cannot be crossed. Since then I have obtained a forked mutation in *funebris*. This character is strikingly similar to the forked known in *virilis* and to those in *melanogaster* and *simulans*. Forked *funebris* and forked *virilis* agree in that the marginal hairs of the wings stand out almost at right angles to the wing-margin itself, instead of lying nearly flat along the wing margin as they do in wild-type flies. This peculiarity is also present in forked *melanogaster* and *simulans*, but is much less marked, i.e., the angle is decidedly less than 90°. It is probable that forked *funebris* is allelomorphic at least to forked *virilis*, though here again the two species cannot be crossed.

Tests of the linkage between notch and forked in *funebris* have given 931 crossovers among 3198 flies, a crossover percentage of 29.1. Allowing for about the amount of double crossing over usual in *melanogaster*, we may provisionally map the two loci about 32 units apart. Notch in *melanogaster* being a little less than 4 units from yellow, the position of forked in *funebris* becomes approximately 36, as opposed to 56.3 in *melanogaster*, 57.2 in *simulans*, and about 56 in *virilis*. There are several possibilities of error in this calculation for *funebris;* but taken at its face value it indicates much less crossing over in the X chromosome of *funebris* than in those of the other three species. This result is rather unexpected, in view of METZ'S (1916) observation that what is presumably the X chromosome of *funebris* is, cytologically, much longer in proportion to the rest of the chromatin than is the X of *melanogaster* or of *virilis*. Of course, since METZ'S observations are based on chromosomes in the contracted stage, it is possible that the finely spun-out growth-stage chromosomes do not show a disproportion in this direction. Even if they do it is quite possible that other factors act to decrease the amount of crossing over in *funebris*. In any case, speculation along these lines is rather futile until more information concerning the *funebris* map is available, i.e., until more sex-linked mutants are discovered and studied.[7]

[7] Since the above was written a mutant gene lying at least 45 units to the right of forked has been studied in *funebris*. The discussion given needs revision accordingly.

THE GENETIC EVIDENCE OF A MULTIPLE (TRIPLE) ALLELOMORPH SYSTEM IN BRUCHUS AND ITS RELATION TO SEX-LIMITED INHERITANCE[1]

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INTRODUCTION

This paper concerns the origin and genetic behavior of four different body colors, which have manifested themselves in my cultures of the so-called "four-spotted cowpea-weevil," *Bruchus quadrimaculatus*, Fabr. The inheritance of these colors involves both allelomorphism and sex-limited inheritance. These colors, red, black, white, and tan, are more apparent

[1] Contribution from the Zoölogical Laboratory of the UNIVERSITY OF OKLAHOMA. The experiments, however, were carried on at WESTERN RESERVE UNIVERSITY and, in part, at the BIOLOGICAL LABORATORY, Cold Spring Harbor, Long Island.

in the females, and less conspicuous in the males, because the latter usually have tan elytra. The males, however, carry the color factors, although they are not manifested to such a marked degree somatically. Experiments prove that these four color types compose a multiple allelomorph system, and that they also form an epistatic series. The order of dominance is red, black, white and tan.

During a search for insects which might be favorable for genetic studies, the possibilities of the Bruchidae were considered because several species were known to breed readily in stored seed and to produce several generations each year. The first experiments with these insects involved a culture of *Bruchus obtectus*, Say., the "common bean-weevil," but these were given up because it was too difficult to distinguish the sexes. It was difficult to obtain living cultures of the so-called "cowpea-weevil," *Bruchus chinensis*, Linn., but it was comparatively easy to procure living *Bruchus quadrimaculatus*, Fabr.

Several reasons may be given why these beetles are adapted for a study in genetics. It is not necessary to etherize them because they letisimulate when poured out of a culture bottle. Likewise, they breed rapidly and may produce a generation within twenty-five days if the temperature is maintained at 30°C, and the relative humidity at about 80 percent. Lastly, these weevils will breed on any species of cowpea, and bottles of any size may be used as containers.

LIFE HISTORY AND DISTRIBUTION

The adults deposit their eggs on the surface of the cowpea. A few days after oviposition the young larva emerges through an opening which it makes in the under side of the egg; it then burrows into the seed, where it feeds until it reaches the pupa stage. It requires about two weeks for the white, legless larva to attain full growth. At the end of about twenty days from time of egg-deposit the pupa state is reached, and this lasts about five days. At first the pupae are white, but after a few days they change to a light tan color. The adult insect emerges through a circular opening which it makes with its jaws. Usually within one day after emergence, the beetles mate and the females lay their eggs.

Since its introduction, this insect has become widely distributed throughout the United States, Mexico, Brazil, the West Indies, and other warm countries. CHITTENDEN (1898) believes that it is probable that this insect, with its preferred food plant, the cowpea, was introduced from the orient. The weevil is found wherever its food plant grows. It will also breed in stored seed if the proper environmental conditions are furnished.

METHODS OF THE EXPERIMENT

The Whippoorwill variety of the cowpea was used for food because it can be obtained at almost any seed store. This seed was put in flasks plugged with cotton and sterilized in an autoclave, to make certain the destruction of any eggs or larvae or adults which might contaminate the experiment. The seeds were then put into bottles which had been boiled for more than twenty minutes, after which they were plugged with cotton, preparatory to their use as breeding chambers. It was found that this species is subject to the attack of the mite, *Pediculoides ventrocosus*, New., which destroys larvae and adults, but this parasite is easily controlled by the sterilization of the food and bottles. One pair of beetles was placed in each container and left until the young emerged. An oven regulated by a thermostat was used to maintain the desired temperature and great care was exercised to keep the proper humidity. The humidity when in excess, affects injuriously both cowpeas and weevils, while if the air is too dry the adults may die, or the eggs, larvae or pupae may be destroyed. A relative humidity of 80 percent proved the most satisfactory. Fresh cowpeas are absolutely essential. The stock cultures were carried on by placing ten females and ten males in a bottle. Virgin females may be obtained by opening infested seed or by using females that have emerged within twelve hours. It is a simple matter to distinguish males from females because of the remarkable sexual dimorphism exhibited in this species.

ORIGIN OF TYPES AND MUTANTS

The insects used were received from the TEXAS AGRICULTURAL EXPERIMENT STATION. They were permitted to interbreed for several generations, to determine their genetic potentialities. The body color of this wild stock in both males and females was tan. In the fourth generation a red female was observed; in the sixth generation a black female was discovered; and a white female appeared in the ninth generation. Other cultures of Bruchus from different parts of the United States have been examined for these types. Professor Z. P. METCALF of the NORTH CAROLINA AGRICULTURAL EXPERIMENT STATION sent stock which already contained several red females and black females, but the tan or wild type greatly predominated. No white mutant originated during more than twenty-three generations. The North Carolina red type and black type were isolated and were found to have the same genetic behavior as the reds and blacks which had apparently appeared as mutants in the wild stock that came from Texas. Dur-

ing the summer of 1918, Adzuki beans which were badly infested with this weevil were obtained through the kindness of Dr. A. F. BLAKESLEE, but his stock, when examined, was all tan, and no evidence of any mutant was found during thirteen generations. Infested cowpeas which had been purchased at a seed store in New York City, contained, among several hundred individuals, two black females.

DESCRIPTION OF SPECIES: THE ORIGIN OF THE FOUR COLOR FACTORS

The family Bruchidae comprises three genera of insects: Spermophagus, Caryoborus, and Bruchus. HORN's (1873) description of *Bruchus quadrimaculatus*, Fabr. follows:

"Elongate oval, moderately shining. Beneath equally clothed with whitish pubescence. Elytra ferruginous or pale brown with large lateral spot and apex broadly black. Head dark brown or black, densely punctured, front sub-carinate. Antennae as long as head and thorax, serrate in both sexes, four basal joints pale rufous, outer joints dark and nearly black. Thorax trapezoidal, broader at base than long, sides distinctly arcuate, base trisinuate, basal lobe emarginate and clothed with whitish hairs; color variable from ferruginous to black, coarsely punctured, subgranulate and feebly shining, sparsely clothed with cinereous hair. Scutellum with median impressed line and clothed with whitish hair. Elytra broader at base than thorax and longer than wide, sides feebly arcuate, humeri moderately prominent; striae punctured, intervals flat, densely punctulate; color ferruginous with large lateral spot and apex black, clothed with whitish and cinereous pubescence. Pygidium nearly black with medium line of whitish pubescence. Body beneath piceous, densely punctulate and sparsely but evenly clothed with cinereous hairs; abdomen pale brown. Anterior and middle legs pale rufous, hind legs pale brown. Hind femora armed with an acute tooth on the inner side and a broad triangular tooth on the outer side. Length 3–4.5 mm."

No specific mention has been made in the literature indicating the existence of different types in this species, yet CHITTENDEN (1898) in describing this insect states that the ground color is black, with black, gray, and white pubescence, and WADE (1919) writes that there is an exceedingly wide range of color, which varies from a dark or almost black, to brown or reddish brown.

DESCRIPTION OF TYPES

The tan type or wild form

The tan female has two black spots near the base of the elytra, similar to those in the red and the white types. The entire body is tan with the usual white-hair distribution. The pronotum and head are black, but the antennae are tan. In size it is smaller than the black mutants but larger

than the reds and whites. The male is likewise tan except for the pronotum, head, and eyes, which are black. He has no spots on his elytra. Short white hairs cover the dorsal and ventral sides. The male and female correspond in color to RIDGEWAY'S "testaceous." In crosses with either red, black or white, tan is recessive. The formula is *rr*, which represents male and female of the wild type.

The red type or mutant

The first appearance of the red type occurred in the fourth generation, where it was discovered in the wild stock which had been bred in large numbers. In this type the females are red and the males vary from light red to tan. It required several generations before a type which bred true was segregated. This was accomplished by mating the first red female with a male of the wild stock, although it was doubtful whether this female was a virgin. The F_1 from this cross produced fifty-three red females and fifty-seven males which varied from light red to tan. This indicated that red was dominant to tan in the females. Ten males and ten females of this F_1 generation were inbred. They produced 138 red females, 57 tan females and 221 tan males in the F_2 generation. This further indicated that red is dominant to tan for the females. The next procedure was to obtain fifty virgin females and to mate them separately with F_2 males. Each pair was placed in a separate bottle. Only two pairs bred true to the red type. Since the other cultures produced both red and tan females, they were discarded.

The entire body of the red female is red except for the head and eyes, which are black. Her elytra are also red either with or without markings. Her color resembles RIDGEWAY'S "Hessian brown," but our common hazelnut approximates the color more closely. The elytra of the male and his entire body are of a red-tan color, except that his head and pronotum are black. It is evident that the sex-limited traits are least conspicuous for this type than for any other.

This red mutant was discovered first and since it belongs to a multiple allelomorph series, it seems advisable to use *RR*, as the formula for this type in both sexes. The red type is dominant to either the black, the white or the tan types, and it can be the allelomorph of any other color factor.

The black type or mutant

When the black female, which was first discovered in the sixth generation of the wild or tan stock, was mated with a tan male of the wild stock, the offspring consisted of 27 black females and 29 tan males. These F_1 indi-

viduals produced 153 black females, 61 tan females and 201 tan males. The result indicates that black is dominant to tan in the females. After many attempts, a homozygous strain for the black type was isolated. It has been bred true for more than forty generations. The black female differs from the tan female by being pure black in color and larger. The male of the black type differs from that of the tan male by being gray underneath and by having a black body. Tan predominates in the elytra of the male of the black type, and is similar to the tan of the wild type. Consequently, there is marked sexual dimorphism in the black type. It is advisable to use R^bR^b to indicate this mutant for both sexes, because it was the second mutant discovered in the multiple allelomorph series. The results will prove that black is dominant to either white, or tan, but recessive to red.

The white type or mutant

The white female made her appearance in the ninth generation of inbred wild stock. This white female was mated with a tan male of the pure tan stock. Four white females and seven tan males were procured. In the F_2 generation these produced 15 white females, 8 tan females, and 32 tan males. This indicated that white is dominant to tan in the females. Several F_2 pairs were mated, using virgin females, and after several cultures one of the pairs bred true for white. This stock has been bred homozygously for about thirty generations.

The female of the white type is covered with white pubescence, except for the head, pronotum and antennae, which are black. Her elytra may manifest two or more black spots. The male is gray in color except for his elytra which are of a light tan color. White is dominant to tan, but recessive to red or black. The formula used is R^wR^w. It is a third member of the multiple allelomorph series.

With reference to size differences, the females are usually larger than the males in all four of the types. The adults vary in length from 3 to 5 mm. The black mutants are the largest and the white ones the smallest. The red mutant is larger than the tan or wild type, and both fall between the black and the white types.

THE FORMULAE

The formulae used in this paper are adapted to meet the experimental results obtained. Since no geneticist has developed formulae to account for the modifications necessitated by the sex-limited traits involved, the formulae used by MORGAN and BRIDGES (1913) are adapted here. The proposed formulae are as follows:

	Females	*Males*
Red type	*RR* (red elytra and body)	*RR* (reddish tan elytra and body)
Black type	R^bR^b (black elytra and body)	R^bR^b (tan elytra, dark gray body)
White type	R^wR^w (white elytra and body)	R^wR^w (light tan elytra, gray body)
Tan or wild type	*rr* (tan elytra and body)	*rr* (tan elytra and body)

THE EXPERIMENTAL RESULTS

Introduction

In the tests and tables which follow all the males are classified as tan, because the elytra of the male usually resembles the tan of the wild type. But the body colors do show differences. Males of the red type usually manifest a red tinge; the black ones, too, show some black pubescence, and the white males are gray in color.

The first six tests (tables 1 to 12) deal with crosses involving these four factors. They prove that any color factor may pair with any other of this series as an allelomorph. The results from these six tests should prove that the dominant females, the recessive females, and the (tan) males in every instance, approximate a 3:1:4 phenotypic ratio in the F_2 generation. The tests 7 to 13 give the results obtained from various back-crosses. They prove that the color factors are carried by the males as well as by the females. The data to further prove that these factors form a multiple allelomorph system are given in tests 13 to 26.

The heredity of red, black, white and tan types involving one pair of factors

Conclusions from mass cultures (tests 1–6; tables 1–12)

The first six tests show that, when any two factors for the four body colors are brought together in pairs, Mendelian segregation takes place, and further, the order of dominance is red, black, white and tan. When two individuals, each carrying a different color factor, are crossed, their F_2 offspring approximate a 3:1:4 phenotype ratio.

TABLE 1

Test 1

P_1 = red ♀ (RR) × tan ♂ (R^bR^b) of the black type.
F_1 = red ♀ (RR^b) × tan ♂ (RR^b).
F_2 = 3 red ♀ (RR, RR^b, RR^b):1 black ♀ (R^bR^b):4 tan ♂ (RR, RR^b, RR^b, R^bR^b).

PEDIGREE NUMBER	F_1		F_2		
	♀ red	♂ tan	♀ red	♀ black	♂ tan
1 (2)[2]	34	35	70	19	74
2	82	77	109	35	129
3 (2)	26	28	56	18	88
28 (2)	22	23	155	51	216
40 (3)	33	51	289	96	351
42 (3)	50	52	299	99	320
43	24	19	133	45	183
50 (5)	47	86	310	106	391
58 (5)	87	88	418	140	599
62	32	35	240	47	267
95 (3)	2	3	13	6	17
152	44	55	532	176	771
153	40	27	366	130	460
154	39	48	532	178	683
193	27	29	176	40	254
194	38	34	231	69	326
256	20	22	657	215	881
257	16	15	286	93	364
269	13	14	336	111	339
308	71	76	551	183	761
309 (2)	44	4	51	21	70
311 (2)	61	54	495	173	748
321 (2)	20	25	390	183	525
322	18	23	307	101	407
Totals.....	850	923	6992	2335	9224
Calculated.....	*887*	*887*	*6957*	*2319*	*9276*

[2] The number in parentheses indicates the number of each sex used in the mass culture. Cultures not thus marked are from single pairs.

TABLE 2

Test 1

P_1 = black ♀ (R^bR^b) × tan ♂ of the red type (RR); F_1 and F_2 as in table 1.

PEDIGREE NUMBER	F_1		F_2		
	♀ red	♂ tan	♀ red	♀ black	♂ tan
27 (2)	33	29	151	49	149
41	19	21	144	56	174
51 (5)	40	40	393	127	504
59 (5)	49	46	217	76	305
63 (6)	44	42	242	80	345
96 (3)	21	24	80	30	82
111	29	26	132	44	199
131 (5)	105	115	461	154	685
149	22	20	165	58	246
187	12	11	49	17	68
251	13	12	163	67	249
252	21	25	506	171	706
255	27	28	328	125	428
306 (2)	68	73	429	163	546
307 (2)	57	60	570	198	662
312 (2)	76	57	546	160	636
314	24	37	186	61	208
315	21	15	227	68	293
317	25	28	314	69	324
318	15	17	659	139	772
Totals	721	726	5863	1912	7581
Calculated	*724*	*724*	*5758*	*1920*	*7678*

TABLE 3

Test 2

P_1 = red ♀ (*RR*) × tan ♂ of the tan type (*rr*).
F_1 = red ♀ (*Rr*) × tan ♂ (*Rr*).
F_2 = 3 red ♀ (*RR*, *Rr*, *Rr*):1 tan ♀ (*rr*):4 tan ♂ (*RR*, *Rr*, *Rr*, *rr*).

PEDIGREE NUMBER	F_1		F_2		
	♀ red	♂ tan	♀ red	♀ tan	♂ tan
5	53	57	138	61	221
19	13	18	114	39	185
52	37	35	191	69	251
56 (5)	49	44	220	85	311
86 (4)	20	22	58	21	68
102	15	14	57	23	99
104	30	33	153	98	254
144	34	31	386	110	519
145	32	32	330	112	482
146	26	45	126	48	199
147	31	32	231	78	338
210	22	19	58	22	83
214	1	6	6	1	7
216	24	25	141	36	201
330	27	26	324	134	482
331	15	18	215	73	316
350	25	22	595	119	721
352	22	29	290	90	381
Totals	476	508	3633	1218	5118
Calculated	*492*	*492*	*3738*	*1246*	*4984*

TABLE 4

Test 2

P_1 = tan ♀ (*rr*) × tan ♂ of the red type (*RR*); F_1 and F_2 as in table 3.

PEDIGREE NUMBER	F_1		F_2		
	♀ red	♂ tan	♀ red	♀ tan	♂ tan
4	24	25	181	60	243
30	12	12	64	16	83
65 (5)	38	39	179	58	260
140	11	14	144	49	215
141	15	20	178	47	244
209	18	19	124	42	123
326	11	14	70	19	97
327	16	28	234	54	258
329	16	21	408	134	562
355	25	23	350	113	502
Totals	186	215	1932	592	2587
Calculated	*201*	*201*	*1917*	*639*	*2556*

TABLE 5

Test 3

P_1 = black ♀ (R^bR^b) × tan ♂ (rr) of the tan type.

F_1 = black ♀ (R^br) × tan ♂ (R^br).

F_2 = 3 black ♀ (R^bR^b, R^br, R^br):1 tan ♀ (rr):4 tan ♂ (R^bR^b, R^br, R^br, rr).

PEDIGREE NUMBER	F_1		F_2		
	♀ black	♂ tan	♀ black	♀ tan	♂ tan
6	27	29	153	57	201
11	4	12	33	12	49
35 (4)	22	22	178	60	272
36 (4)	24	21	78	24	153
38 (4)	53	57	230	63	274
46 (5)	48	38	175	60	244
48 (4)	12	6	42	22	63
54 (5)	48	51	164	44	176
60 (5)	52	50	244	96	325
66 (5)	87	86	436	195	668
105	31	31	104	51	151
134	19	36	243	81	308
136	20	22	278	94	330
211	18	18	68	29	93
213 (2)	49	48	176	60	191
310	20	30	285	100	339
313	21	19	237	77	275
323	16	18	222	71	326
325	11	12	240	86	353
Totals.....	582	606	3586	1282	4791
Calculated.....	*594*	*594*	*3622*	*1207*	*4830*

TABLE 6

Test 3

P_1 = tan ♀ (rr) × tan ♂ (R^bR^b) of the black type; F_1 and F_2 as in table 5.

PEDIGREE NUMBER	F_1		F_2		
	♀ black	♂ tan	♀ black	♀ tan	♂ tan
37 (3)	48	62	181	65	239
47 (3)	21	25	69	23	94
49 (3)	14	21	23	8	21
55 (5)	10	19	31	9	45
57 (5)	68	71	230	98	341
61 (5)	15	13	52	18	84
67 (4)	39	39	97	31	138
97 (3)	20	17	102	37	113
132	33	25	272	82	230
137	27	26	91	20	126
223	13	14	274	61	328
224	3	4	86	4	81
225	18	19	122	41	200
Totals.....	329	355	1632	497	2040
Calculated.....	*342*	*342*	*1563*	*521*	*2085*

TABLE 7

Test 4

P_1 = red ♀ (RR) × tan ♂ (R^wR^w) of the white type.
F_1 = red ♀ (RR^w) × tan ♂ (RR^w).
F_2 = 3 red ♀ (RR, RR^w, RR^w):1 white ♀ (R^wR^w):4 tan ♂ (RR, RR^w, RR^w, R^wR^w).

PEDIGREE NUMBER	F_1		F_2		
	♀ red	♂ tan	♀ red	♀ white	♂ tan
7	10	10	47	12	61
83	11	12	63	30	95
87 (2)	24	18	129	64	195
89 (3)	37	33	220	74	301
100	13	18	37	14	54
156	25	26	276	92	383
157	26	23	233	81	311
158	30	32	118	37	163
159	2	4	37	14	52
160	23	27	77	23	106
161	32	39	301	114	416
162	28	26	80	28	108
231	15	14	94	33	147
232	32	33	455	152	603
234	35	31	319	146	472
235	30	32	199	77	370
348	47	40	686	262	980
Totals.....	420	418	3371	1253	4817
Calculated.....	*419*	*419*	*3540*	*1180*	*4720*

TABLE 8

Test 4

P_1 = white ♀ (R^wR^w) × tan ♂ (RR) of the red type; F_1 and F_2 as in table 7.

PEDIGREE NUMBER	F_1		F_2		
	♀ red	♂ tan	♀ red	♀ white	♂ tan
70 (2)	23	26	69	22	92
163	11	9	70	24	88
164	20	13	132	62	311
166	27	19	283	85	323
171	2	1	3	1	7
172	20	34	94	22	161
178	34	21	135	47	190
201	2	2	8	3	14
203	10	11	31	12	60
229	3	2	42	16	51
303	8	15	56	15	49
Totals.....	160	153	923	309	1346
Calculated.....	*156*	*156*	*967*	*322*	*1289*

TABLE 9

Test 5

P_1 = black ♀ (R^bR^b) × tan ♂ (R^wR^w) of the white type.
F_1 = black ♀ (R^bR^w) × tan ♂ (R^bR^w).
F_2 = 3 black ♀ (R^bR^b, R^bR^w, R^bR^w):1 white ♀ (R^wR^w):4 tan ♂ (R^bR^b, R^bR^w, R^bR^w, R^wR^w).

PEDIGREE NUMBER	F_1		F_2		
	♀ black	♂ tan	♀ black	♀ white	♂ tan
74 (5)	43	42	118	31	79
90 (3)	23	17	66	27	82
91 (3)	62	54	187	57	228
92 (3)	22	34	128	42	171
173	33	32	122	40	180
177	29	30	12	2	15
186	17	21	117	33	141
199	15	6	207	36	208
249	25	16	308	135	427
Totals.....	292	272	1413	502	1766
Calculated.....	*282*	*282*	*1227*	*409*	*1636*

TABLE 10

Test 5

P_1 = white ♀ (R^wR^w) × tan ♂ (R^bR^b) of the black type; F_1 and F_2 as in table 9.

PEDIGREE CULTURE	F_1		F_2		
	♀ black	♂ tan	♀ black	♀ white	♂ tan
72 (2)	25	27	45	8	52
73 (4)	17	18	5	1	4
93 (3)	14	16	50	17	46
94 (3)	36	39	47	23	48
246	11	16	127	37	105
247	3	1	25	13	44
284	9	10	122	45	168
289	15	10	56	17	78
339	11	17	89	35	115
Totals.....	141	154	566	196	660
Calculated.....	*147*	*147*	*574*	*158*	*732*

TABLE 11

Test 6

P_1 = white ♀ (R^wR^w) × tan ♂ (rr) of the tan type.
F_1 = white ♀ (R^wr) × tan ♂ (R^wr).
F_2 = 3 white ♀ (R^wR^w, R^wr, R^wr):1 tan ♀ (rr):4 tan ♂ (R^wR^w, R^wr, R^wr, rr).

PEDIGREE NUMBER	F_1		F_2		
	♀ white	♂ tan	♀ white	♀ tan	♂ tan
22	3	3	21	16	21
75 (3)	20	24	124	28	155
76 (4)	20	19	111	49	175
218	13	8	55	20	86
270	5	6	13	4	19
271	1	12	91	20	133
274	19	17	179	52	273
Totals	81	89	594	189	862
Calculated	*85*	*85*	*618*	*206*	*824*

TABLE 12

Test 6

P_1 = tan ♀ (rr) × tan ♂ (R^wR^w) of the tan type; F_1 and F_2 as in table 11.

PEDIGREE NUMBER	F_1		F_2		
	♀ white	♂ tan	♀ white	♀ tan	♂ tan
78 (4)	34	31	48	22	60
81 (4)	17	12	35	11	34
206	22	28	83	20	125
Totals	73	71	166	53	219
Calculated	*72*	*72*	*165*	*55*	*220*

Back-cross tests and the heredity of the four body colors

Conclusions from back-cross tests (tests 7 to 13; tables 13 to 19)

These crosses show that any two of the four color factors may stand in relation of allelomorphs to each other. The results also demonstrate that the order of dominance, as previously given, is red, black, white, and tan. Polymorphism and sex-limited inheritance are also manifested. The following tests give further proof.

TABLE 13

Test 7: Red, heterozygous for red and white, by homozygous red.

P_1 = red ♀ (RR^w) × tan ♂ (RR) of the red type: five pairs mated.
F_1 = red ♀ (RR, RR^w, totals 148): tan ♂ (RR, RR^w, totals 121).

Reciprocal cross

P_1 = red ♀ (RR) × tan ♂ (RR^w) of a red-white combination: five pairs mated.
F_1 = red ♀ (RR, RR^w; totals 166): tan ♂ (RR, RR^w; totals 163).

TABLE 14

Test 8: Red, heterozygous for red and white, by homozygous white.

P_1 = red ♀ (RR) × tan ♂ (R^wR^w) of the white type.
F_1 = 1 red ♀ (RR^w):1 white ♀ (R^wR^w):2 tan ♂ (RR^w, R^wR^w).

CULTURE NUMBER	RED ♀ (RR^w)	WHITE ♀ (R^wR^w)	TAN ♂ (RR^w, R^wR^w)
1046	16	19	44
1054	2	6	5
1055	9	6	15
1056	5	9	5
1057	18	11	49
Totals.....	50	51	111
Calculated.....	*53*	*53*	*106*

Reciprocal cross

P_1 = white ♀ (R^wR^w) × tan ♂ (RR^w) of a red-white combination.
F_1 = Same as above.

CULTURE NUMBER	RED ♀ (RR^w)	WHITE ♀ (R^wR^w)	TAN ♂ (RR^w, R^wR^w)
2031	13	15	29
2036	26	22	44
2037	5	4	21
15611	6	11	14
15612	3	1	5
16170	9	8	11
Totals.....	62	61	124
Calculated.....	*62*	*62*	*124*

TABLE 15

Test 9: Red, heterozygous for red and black, by homozygous black.

P_1 = red ♀ (RR^b) × tan ♂ (R^bR^b) of the black type.
F_1 = 1 red ♀ (RR^b):1 black ♀ (R^bR^b):2 tan ♂ (RR^b, R^bR^b).

CULTURE NUMBER	RED ♀ (RR^b)	BLACK ♀ (R^bR^b)	TAN ♂ (RR^b, R^bR^b)
1012	29	31	26
1013	16	21	42
1014	12	24	53
1029	30	22	25
1030	19	26	45
1031	18	19	39
1032	3	1	1
1047	12	18	25
1048	20	10	28
1521	7	5	15
1536	20	21	42
1577	22	28	25
Totals	208	226	368
Calculated	*201*	*201*	*402*

Reciprocal cross

P_1 = black ♀ (R^bR^b) × tan ♂ (RR^b) of a red-black combination.
F_1 = Same as above.

CULTURE NUMBER	RED ♀ (RR^b)	BLACK ♀ (R^bR^b)	TAN ♂ (RR^b, R^bR^b)
1311	2	3	1
1004	10	8	41
1008	14	16	26
1026	44	42	106
1027	23	13	49
1028	19	18	35
1029	22	21	39
Totals	134	121	297
Calculated	138	*138*	*276*

TABLE 16

Test 10: Black, heterozygous for black and tan, by homozygous tan.

P_1 = black ♀ ($R^b r$) × tan ♂ (rr) of the tan type.
F_1 = 1 black ♀ ($R^b R$): 1 tan ♀ (rr): 2 tan ♂ ($R^b r$, rr).

CULTURE NUMBER	BLACK ♀ ($R^b r$)	TAN ♀ (rr)	TAN ♂ ($R^b r$, rr)
1023	13	18	47
1362	33	31	64
1377	29	22	43
1379	13	17	32
Totals	88	88	186
Calculated	*90*	*90*	*180*

Reciprocal cross

P_1 = tan ♀ (rr) × tan ♂ ($R^b r$) of a black-tan combination.
F_1 = Same as above.

CULTURE NUMBER	BLACK ♀ ($R^b r$)	TAN ♀ (rr)	TAN ♂ ($R^b r$, rr)
1345	3	8	17
1347	2	5	14
1365	5	1	2
1367	7	4	9
13611	9	11	21
13614	6	4	11
Totals	32	33	64
Calculated	*32*	*32*	*64*

TABLE 17

Test 11: Black, heterozygous for black and white, by homozygous white.

P_1 = black ♀ ($R^b R^w$) × tan ♂ ($R^w R^w$) of the white type.
F_1 = 1 black ♀ ($R^b R^w$): 1 white ♀ ($R^w R^w$): 2 tan ♂ ($R^b R^w$, $R^w R^w$).

CULTURE NUMBER	BLACK ♀ ($R^b R^w$)	WHITE ♀ ($R^w R^w$)	TAN ♂ ($R^b R^w$, $R^w R^w$)
1041	14	12	30
1042	12	10	19
1043	16	22	36
1044	18	16	33
1045	12	13	35
Totals	72	73	153
Calculated	*74*	*74*	*148*

Reciprocal cross

P_1 = white ♀ ($R^w R^w$) × tan ♂ ($R^b R^w$) of a black-white combination.
F_1 = Same as above.

CULTURE NUMBER	BLACK ♀ ($R^b R^w$)	WHITE ♀ ($R^w R^w$)	TAN ♂ ($R^b R^w$, $R^w R^w$)
1993	5	6	12
2005	17	18	33
2006	22	19	39
2007	24	27	52
2008	19	20	38
Totals	87	90	174
Calculated	*88*	*88*	*176*

TABLE 18

Test 12: White, heterozygous for white and tan, by homozygous tan.

P_1 = white ♀ ($R^w r$) × tan ♂ (rr) of the tan type.
F_1 = 1 white ♀ ($R^w r$) : 1 tan ♀ (rr) : 2 tan ♂ ($R^w r$, rr).

CULTURE NUMBER	WHITE ♀ ($R^w r$)	TAN ♀ (rr)	TAN ♂ ($R^w r$, rr)
1058	15	15	29
1060	10	11	23
2016	19	20	40
2017	8	9	18
2018	13	12	24
Totals	65	67	134
Calculated	*67*	*67*	*134*

Reciprocal cross

P_1 = tan ♀ (rr) × tan ♂ ($R^w r$) of a white-tan combination.
F_1 = Same as above.

CULTURE NUMBER	WHITE ♀ ($R^w r$)	TAN ♀ (rr)	TAN ♂ ($R^w r$, rr)
1034	3	4	6
1036	6	13	19
2019	10	6	19
2020	16	17	34
1049	12	11	22
Totals	47	51	100
Calculated	*50*	*50*	*100*

TABLE 19

Test 13: Red, heterozygous for red and tan, by homozygous tan.

P_1 = red ♀ (Rr) × tan ♂ (rr) of the tan type.
F_1 = 1 red ♀ (Rr) : 1 tan ♀ (rr) : 2 tan ♂ (Rr, rr).

CULTURE NUMBER	RED ♀ (Rr)	TAN ♀ (rr)	TAN ♂ (Rr, rr)
2031	15	16	32
2032	19	18	35
2033	10	9	20
2034	17	19	36
2035	20	21	42
Totals	81	83	165
Calculated	*82*	*82*	*164*

Reciprocal cross

P_1 = tan ♀ (rr) × tan ♂ (Rr) of a red-tan combination.
F_1 = Same as above.

CULTURE NUMBER	RED ♀ (Rr)	TAN ♀ (rr)	TAN ♂ (Rr, rr)
2036	21	20	42
2037	18	19	37
2038	14	12	25
2039	12	13	24
2040	16	16	31
Totals	81	80	159
Calculated	*80*	*80*	*160*

The genetic behavior of hybrid crosses involving three factors in relation to a multiple allelomorph series

Conclusions based on the preceding crosses involving three color factors (tests 13 to 24; tables 20 to 30)

When a Bruchid which is heterozygous for any two color factors, is mated with a homozygous individual carrying a third color factor, the progeny will approximate a 1:1 ratio or a 1:1:2 ratio. These ratios are, of course, typical sex-limited ones.

This group of tests furnishes proof that the four color factors form a system of multiple allelomorphs, for it is evident that only two of these factors can exist at any one time in any one individual, and since the elytra colors are sex-limited, they are not manifested in the males.

TABLE 20

Test 14: White, heterozygous for white and tan, by homozygous red.

P_1 = white ♀ (R^wr) × tan ♂ (RR) of the red type; two pairs mated.
F_1 = 1 red ♀ (RR^w, Rr; totals 32):1 tan ♂ (RR^w, Rr; totals 31).

Reciprocal cross

P_1 = red ♀ (RR) × tan ♂ (R^wr) of a white-tan combination; five pairs mated.
F_1 = 1 red ♀ (RR^w, Rr; totals 93):1 tan ♂ (RR^w, Rr; totals 68).

TABLE 21

Test 15: Black, heterozygous for black and white, by homozygous tan.

P_1 = black ♀ (R^bR^w) × tan ♂ (rr) of the tan type; six pairs mated.
F_1 = 1 black ♀ (R^br; totals 75):1 white ♀ (R^wr; totals 96):2 tan ♂ (R^br, R^wr; totals 184).

Reciprocal cross

P_1 = tan ♀ (rr) × tan ♂ (R^bR^w) of a black-white combination; seven pairs mated.
F_1 = 1 black ♀ (R^br; totals 50):1 white ♀ (R^wr; totals 50):2 tan ♂ (R^br, R^wr; totals 74).

TABLE 22

Test 16: Black, heterozygous for black and tan, by homozygous white.

P_1 = black ♀ (R^br) × tan ♂ (R^wR^w) of the white type; six pairs mated.
F_1 = 1 black ♀ (R^bR^w; totals 122):1 white ♀ (R^wr; totals 121):2 tan ♂ (R^bR^w, R^wr; totals 248).

Reciprocal cross

P_1 = white ♀ (R^wR^w) × tan ♂ (R^br) of a black-tan combination; two pairs mated.
F_1 = 1 black ♀ (R^bR^w; totals 36):1 white ♀ (R^wr; totals 40):2 tan ♂ (R^bR^w, R^wr; totals 79).

TABLE 23

Test 17: Red, heterozygous for red and white, by homozygous tan.

P_1 = red ♀ (RR^w) × tan ♂ (rr) of the tan type; seven pairs mated.
F_1 = 1 red ♀ (Rr; totals 144):1 white ♀ (R^wr; totals 137):2 tan ♂ (Rr, R^wr; totals 268).

Reciprocal cross

P_1 = tan ♀ (rr) × tan ♂ (RR^w) of a red-white combination; five pairs mated.
F_1 = 1 red ♀ (Rr; totals 78):1 white ♀ (R^wr; totals 70):2 tan ♂ (Rr, R^wr; totals 184).

TABLE 24

Test 18: Red, heterozygous for red and white, by homozygous black.

P_1 = red ♀ (RR^w) × tan ♂ (R^bR^b) of the black type; six pairs mated.
F_1 = 1 red ♀ (RR^b; totals 104):1 black ♀ (R^bR^w; totals 90):2 tan ♂ (RR^b, R^bR^w; totals 197).

Reciprocal cross

P_1 = black ♀ (R^bR^b) × tan ♂ (RR^w) of a red-white combination; four pairs mated.
F_1 = 1 red ♀ (RR^b; totals 53):1 black ♀ (R^bR^w; totals 51):2 tan ♂ (RR^b, R^bR^w; totals 121).

TABLE 25

Test 19: Red, heterozygous for red and black, by homozygous tan.

P_1 = red ♀ (RR^b) × tan ♂ (rr) of the tan type; six pairs mated.
F_1 = 1 red ♀ (Rr; totals 97):1 black ♀ (R^br: totals 79):2 tan ♂ (Rr, R^br; totals 194).

Reciprocal cross

P_1 = tan ♀ (rr) × tan ♂ (RR^b) of a red-black combination; three pairs mated.
F_1 = 1 red ♀ (Rr; totals 34):1 black ♀ (R^br; totals 22):2 tan ♂ (Rr, R^br; totals 48).

TABLE 26

Test 20: Red, heterozygous for red and black, by homozygous white.

P_1 = red ♀ (RR^b) × tan ♂ (R^wR^w) of the white type; four pairs mated.
F_1 = 1 red ♀ (RR^w; totals 39):1 black ♀ (R^bR^w; totals 33):2 tan ♂ (RR^w, R^bR^w; totals 76).

Reciprocal cross

P_1 = white ♀ (R^wR^w) × tan ♂ (RR^b) of a red-black combination; four pairs mated.
F_1 = 1 red ♀ (RR^w; totals 36): 1 black ♀ (R^bR^w; totals 36): 2 tan ♂ (RR^w, R^bR^w; totals 69).

TABLE 27

Test 21: Black, heterozygous for black and tan, by homozygous red.

P_1 = black ♀ (R^br) × tan ♂ (RR) of the red type; five pairs mated.
F_1 = 1 red ♀ (RR^b, Rr; totals 204): 1 tan ♂ (RR^b, Rr; totals 192).

Reciprocal cross

P_1 = red ♀ (RR) × tan ♂ (R^br) of a black-tan combination; four pairs mated.
F_1 = 1 red ♀ (RR^b, Rr; totals 166): 1 tan ♂ (RR^b, Rr; totals 200).

TABLE 28

Test 22: Black, heterozygous for black and white, by homozygous red.

P_1 = black ♀ (R^bR^w) × tan ♂ (RR) of the red type; six pairs mated.
F_1 = red ♀ (RR^b, RR^w; totals 217):tan ♂ (RR^b, RR^w; totals 227).

Reciprocal cross

P_1 = red ♀ (RR) × tan ♂ (R^bR^w) of a black-white combination; three pairs mated.
F_1 = 1 red ♀ (RR^b, RR^w; totals 50): 1 tan ♂ (RR^b, RR^w; totals 36).

TABLE 29

Test 23: White, heterozygous for white and tan, by homozygous black.

P_1 = white ♀ (R^wr) × tan ♂ (R^bR^b) of the black type; two pairs mated.
F_1 = 1 black ♀ (R^bR^w, R^br; totals 51): 1 tan ♂ (R^bR^w, R^br; totals 40).

Reciprocal cross

P_1 = black ♀ (R^bR^b) × tan ♂ (R^wr) of a white-tan combination; seven pairs mated.
F_1 = 1 black ♀ (R^bR^w, R^br; totals 155): 1 tan ♂ (R^bR^w, R^br; totals 142).

TABLE 30

Test 24: Red, heterozygous for red and tan, by homozygous black.

P_1 = black ♀ (R^bR^b) × tan ♂ (Rr) of a red-tan combination; four pairs mated.
F_1 = 1 red ♀ (RR^b; totals 56):1 black ♀ (R^br; totals 61):2 tan ♂ (RR^b, R^br; totals 123).

Further proof of a multiple allelomorph series by the genetic behavior of two hybrid crosses

Conclusions based on hybrid crosses involving four factors for body color (tests 25 to 36; tables 31 to 42)

It is again evident from these tests that only two of the factors for body color can exist at any one time in any individual. This is a proof of a multiple allelomorph system. The reciprocal crosses prove that the males carry the same combinations as the females, although they are not conspicuous in their phenotypes. The ratios derived from this group of tests are 1:1:2, 2:1:1:4, and 3:1:4; these ratios give evidence of sex-limitation.

TABLE 31

Test 25: Red, heterozygous for red and black, by white, heterozygous for white and tan.

P_1 = red ♀ (RR^b) × tan ♂ (R^wr); eleven pairs mated.
F_1 = 1 red ♀ (RR^w, Rr; totals 190):1 black ♀ (R^bR^w, R^br; totals 196):2 tan ♂ (RR^w, Rr, R^bR^w, R^br; totals 311).

Reciprocal cross

P_1 = white ♀ (R^wr) × tan ♂ (RR^b); nine pairs mated.
F_1 = 1 red ♀ (RR^w, Rr; totals 167):1 black ♀ (R^bR^w, R^br; totals 119):2 tan ♂ (RR^w, Rr, R^bR^w, R^br; totals 375).

TABLE 32

Test 26: Red, heterozygous for red and black, by black, heterozygous for black and white.

P_1 = red ♀ (RR^b) × tan ♂ (R^bR^w); six pairs mated.
F_1 = 1 red ♀ (RR^b, RR^w; totals 88):1 black ♀ (R^bR^b, R^bR^w; totals 86):2 tan ♂ (RR^b, RR^w, R^bR^b, R^bR^w; totals 148).

Reciprocal cross

P_1 = black ♀ (R^bR^w) × tan ♂ (RR^b); five pairs mated.
F_1 = 1 red ♀ (RR^b, RR^w; totals 95):1 black ♀ (R^bR^b, R^bR^w; totals 91):2 tan ♂ (RR^b, RR^w, R^bR^b, R^bR^w; totals 179).

TABLE 33

Test 27: Red, heterozygous for red and black, by black, heterozygous for black and tan.

P_1 = red ♀ (RR^b) × tan ♂ (R^br); nine pairs mated.
F_1 = 1 red ♀ (RR^b, Rr; totals 185):1 black ♀ (R^bR^b, R^br; totals 182):2 tan ♂ (RR^b, Rr, R^bR^b, R^br; totals 346).

Reciprocal cross

P_1 = black ♀ (R^br) × tan ♂ (RR^b); nine pairs mated.
F_1 = 1 red ♀ (RR^b, Rr; totals 176):1 black ♀ (R^bR^b, R^br; totals 174):2 tan ♂ (RR^b, Rr, R^bR^b, R^br; totals 383).

TABLE 34

Test 28: White, heterozygous for white and tan, by red, heterozygous for red and white.

P_1 = white ♀ (R^wr) × tan ♂ (RR^w); two pairs mated.
F_1 = 1 red ♀ (RR^w, Rr; totals 24):1 white ♀ (R^wR^w, R^wr; totals 30):2 tan ♂ (RR^w, Rr, R^wR^w, R^wr; totals 89).

TABLE 35

Test 29: Red, heterozygous for red and tan, by black, heterozygous for black and tan.

P_1 = red ♀ (Rr) × tan ♂ (R^br); twelve pairs mated.
F_1 = 2 red ♀ (RR^b, Rr; totals 161):1 black ♀ (R^br; totals 83):1 tan ♀ (rr; totals 89):4 tan ♂ (RR^b, Rr, R^br, rr; totals 345).

Reciprocal cross

P_1 = black ♀ (R^br) × tan ♂ (Rr); six pairs mated.
F_1 = 2 red ♀ (RR^b, Rr; totals 151):1 black ♀ (R^br; totals 49):1 tan ♀ (rr; totals 61):4 tan ♂ (RR^b, Rr, R^br, rr; totals 249)

TABLE 36

Test 30: Red, heterozygous for red and white, by black, heterozygous for black and tan.

P_1 = red ♀ (RR^w) × tan ♂ (R^br); eleven pairs mated.
F_1 = 2 red ♀ (RR^b, Rr; totals 179):1 black ♀ (R^bR^w; totals 59):1 white ♀ (R^wr; totals 78):4 tan ♂ (RR^b, Rr, R^bR^w, R^wr; totals 320).

Reciprocal cross

P_1 = black ♀ (R^br) × tan ♂ (RR^w); nine pairs mated.
F_1 = 2 red ♀ (RR^b, Rr; totals 154):1 black ♀ (R^bR^w; totals 62):1 white ♀ (R^wr; totals 67): 4 tan ♂ (RR^b, Rr, R^bR^w, R^wr; totals 307).

TABLE 37

Test 31: Black, heterozygous for black and white, by red, heterozygous for red and white.

P_1 = black ♀ (R^bR^w) × tan ♂ (RR^w); seven pairs mated.
F_1 = 2 red ♀ (RR^b, RR^w; totals 74):1 black ♀ (R^bR^w; totals 40):1 white ♀ (R^wR^w; totals 39):4 tan ♂ (RR^b, RR^w, R^bR^w, R^wR^w; totals 198).

Reciprocal cross

P_1 = red ♀ (RR^w) × tan ♂ (R^bR^w); seven pairs mated.
F_1 = 2 red ♀ (RR^b, RR^w; totals 95):1 black ♀ (R^bR^w; totals 53):1 white ♀ (R^wR^w; totals 48):4 tan ♂ (RR^b, RR^w, R^bR^w, R^wR^w; totals 236).

TABLE 38

Test 32: Black, heterozygous for black and tan, by white, heterozygous for white and tan.

P_1 = black ♀ (R^br) × tan ♂ (R^wr); eight pairs mated.
F_1 = 2 black ♀ (R^bR^w, R^br; totals 127):1 white ♀ (R^wr; totals 51):1 tan ♀ (rr; totals 52) : 4 tan ♂ (R^bR^w, R^br, R^wr, rr; totals 245).

Reciprocal cross

P_1 = white ♀ (R^wr) × tan ♂ (R^br); five pairs mated.
F_1 = 2 black ♀ (R^bR^w, R^br; totals 52):1 white ♀ (R^wr; totals 26):1 tan ♀ (rr; totals 31) : 4 tan ♂ (R^bR^w, R^br, R^wr, rr: totals 147).

TABLE 39

Test 33: Red, heterozygous for red and tan, by black, heterozygous for black and white.

P_1 = red ♀ (Rr) × tan ♂ (R^bR^w); fourteen pairs mated.
F_1 = 2 red ♀ (RR^b, RR^w; totals 159):1 black ♀ (R^br; totals 79):1 white ♀ (R^wr; totals 68):4 tan ♂ (RR^b, RR^w, R^br, R^wr; totals 287).

Reciprocal cross

P_1 = black ♀ (R^bR^w) × tan ♂ (Rr); one pair mated.
F_1 = 2 red ♀ (RR^b, RR^w; totals 21):1 black ♀ (R^br; totals 9):1 white ♀ (R^wr; totals 11):4 tan ♂ (RR^b, RR^w, R^br, R^wr; totals 47).

TABLE 40

Test 34: White, heterozygous for white and tan, by red, heterozygous for red and tan.

P_1 = white ♀ (R^wr) × tan ♂ (Rr); one pair mated.
F_1 = 2 red ♀ (RR^w, Rr; totals 13):1 white ♀ (R^wr; totals 6):1 tan ♀ (rr; totals 5):4 tan ♂ (RR^w, Rr, R^wr, rr; totals 19).

TABLE 41

Test 35: Red, heterozygous for red and white, by red, heterozygous for red and tan.

P_1 = red ♀ (RR^w) × tan ♂ (Rr); seven pairs.
F_1 = 3 red ♀ (RR, RR^w, Rr; totals 160): 1 white ♀ (R^wr; totals 54): 4 tan ♂ (RR, RR^w, Rr, R^wr; totals 214.)

Reciprocal cross

P_1 = red ♀ (Rr) × tan (RR^w); one pair mated.
F_1 = 3 red ♀ (RR, RR^w, Rr; totals 5): 1 white ♀ (R^wr; totals 2): 4 tan ♂ (RR, RR^w. Rr, R^wr; totals 11).

TABLE 42

Test 36: Red, heterozygous for red and tan, by red, heterozygous for red and black.

P_1 = red ♀ (Rr) × tan ♂ (RR^b); seven pairs mated.
F_1 = 3 red ♀ (RR, RR^b, Rr; totals 167): 1 black ♀ (R^br; totals 44): 4 tan ♂ (RR, RR^b, Rr, R^br; totals 234).

Reciprocal cross

P_1 = red ♀ (RR^b) × tan ♂ (Rr); one pair mated.
F_1 = 3 red ♀ (RR, RR^b, Rr; totals 36): 1 black ♀ (R^br; totals 16): 4 tan ♂ (RR, RR^b, Rr, R^br; totals 54).

DISCUSSION

The following arguments, taken from MORGAN, STURTEVANT, MULLER and BRIDGES (1915) are in favor of a multiple allelomorph series:

1. That multiple allelomorphs seem to affect the same character. This is true for Bruchus, since the four body colors (red, black, white and tan) affect the entire color pattern.

2. That an individual may contain only two of the genes of the allelomorphic series. These may be the same gene or different members of the allelomorphic series. This behavior is manifested in Bruchus.

3. When any two mutant types of an allelomorphic series are crossed they give a type in the F_1 that is like the dominant parent or intermediate, because neither brings in the normal allelomorph of the other; consequently the wild type is not reconstituted. This relationship holds for the red, black and white mutant types of Bruchus.

4. There is no crossing over between the members of a multiple allelomorph series since such genes occupy the same locus. No crossing over takes place between the four body colors of Bruchus.

In all these four respects the mutants of Bruchus fulfill the requirements of a multiple allelomorph series.

In view of the observation that color dominance appears in the order of red, black, white and tan, it occurred to the writer that it might be interesting to note the correlation, if any, of this color dominance with such physiological traits as vigor, number of progeny, size and the like. As far as can be ascertained, the eggs of these four types are exactly similar in size and color. In the mature beetles, it was discovered that the blacks have the greatest number of progeny, and are most vigorous; the reds follow next in number of offspring and vigor; the tans (or wild type) are next in order, while the white ones rank fourth, because of a seeming lack of vigor and reproductive power. The types in order of size, are black, tan, red and white. There is, further, a marked variation as regards color in these types; for the whites may approach the blacks and the reds may verge on the whites as well as on the tans. Great care is therefore necessary to avoid chance errors in classification.

The sexual dimorphism found in Bruchus is similar to one discovered in Drosophila. The following quotation from MORGAN (1916) is pertinent:

> "A mutant appeared in which the eye color of the female was different from that of the male. The eye color of the female is a dark eosin color, that of the male yellowish eosin. From the beginning this difference was as marked as it is today. Breeding experiments show that eosin eye color differs from the red color of the eye of the wild fly by a single mutant factor. Here, then, at a single step a type appeared that was sexually dimorphic."

It is evident that the color types in Bruchus manifest a similar behavior.

Another interpretation could be put on this sexual dimorphism in Bruchus, which could be made to account for this sex-limitation in color. FOOT and STROBELL (1913) discovered a sex-limited trait in two species of Hemiptera. In one species both sexes were without a spot, while the males in the second species carried a spot. In regard to this MORGAN (1919) states that the results are explicable on the assumption that a single dominant factor, not sex-linked, causes the spot in the males, but the

presence of the gene in the female produces no effect; consequently, the effect is sex-limited and its expression is determined by the rest of the hereditary complex in male or female. This interpretation would likewise account for the results obtained in Bruchus. In this connection, another quotation from MORGAN and his associates (MORGAN, STURTEVANT, MULLER and BRIDGES 1915) is noteworthy:

"Thus while the accessory sexual organs, as well as the secondary sexual characters, may be modified by special differentiators that are not present in the sex chromosomes; yet the sex factor also produces an effect on their development which is different according to whether the sex factor exists in single or double amount."

The results obtained in Bruchus are very similar to the sex-limited inheritance found in Ayrshire cattle as interpreted by WENTWORTH (1916). It is of interest in this connection to quote the author:

"Two general types of inheritance as related to sex exist, aside from the ordinary secondary sex characters. Sex-linked inheritance depends on the great mass of hereditary factors that have been shown to be linked in transmission to the sex-determining factors; while sex-limited factors follow the simple Mendelian scheme of inheritance, but show a reversal of dominance in the two sexes."

The nearest genetic evidence related to this problem is found in the observations on the Java butterfly (*Papilio memnon*, L.) by JACOBSON. These results were discussed in detail by DE MEIJERE (1910), who applied Mendelian principles to these experiments.

To quote MORGAN (1914):

"DE MEIJERE accounts for the results of matings in this species, recorded by JACOBSON, on the assumption of three factors, one for each type of female. The three factors are treated as allelomorphs, and therefore only two of them can be present in any individual, and since they are allelomorphs they pass into different gametes. The order of dominance is Achates, Agenor, Laomedon. The male carries the same factors, but they are not effective in him."

The genetic behavior in Bruchus is somewhat similar to that obtained for Papilio, except that in the former four factors are involved and in the latter only three.

CONCLUSIONS

1. This paper presents the genetic basis of the inheritance of four body and elytra colors in *Bruchus quadrimaculatus*, Fabr.

2. The results prove for Bruchus that any color factor can be an allelomorph with any other factor for body color. The order of dominance is red, black, white, and tan.

3. The four factors (R, R^b, R^w, and r) for the four body colors (red, black, white and tan) constitute a multiple allelomorph system.

4. Sexual dimorphism is exhibited in this species.

5. The life-history studies indicate that this weevil is favorable for genetic researches.

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CONCERNING THE INHERITANCE OF GREEN AND YELLOW PIGMENTS IN MAIZE SEEDLINGS[1]

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INTRODUCTION

The inheritance of green and yellow pigments in maize, as demonstrated by the hereditary behavior of certain abnormal chlorophyll-types of seedlings, has been resolved into a fairly simple hypothesis that suggests some interesting relations between these two types of pigments. Green plastid color in the leaves seems to be governed by two pairs of genetic factors and yellow (presumably xanthophyll and carotin) pigment by one. These three pairs of factors appear to be fundamental in the development of these pigments, although there is some evidence of one or two additional factors.

Three general types of abnormal seedlings are common in fields of maize, namely the albino or pure white, the virescent or greenish-white, and the yellow. The first two possess no visible signs of a definite yellow color upon germinating, while the third exhibits a striking lemon-yellow pigment which probably is a mixture of xanthophyll and carotin. The distinction between these three types is remarkably sharp, especially when they are

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grown under uniform conditions in the greenhouse during the winter months. When grown in the field, the distinction between virescent-white and certain types of yellow seedlings is less marked because the virescent type becomes green or yellowish-green very rapidly under field conditions.

All three seedling types are inherited as simple Mendelian recessives to normal green. The interrelations of the three factor-pairs that govern their inheritance have been definitely determined and form the basis for this publication. Their genetic relation to aleurone color is also discussed. Their group relations are verified by two sets of experiments which prove the independent inheritance of these three pairs of factors.

SUMMARY OF PREVIOUS WORK WITH SEEDLING CHLOROPHYLL-FACTORS

White and virescent-white relation (WwVv)

The first experiments which established the interrelations between the two seedling factors concerned in chlorophyll development of maize, were reported by MILES (1915). These were the *w* and *v* factors, originally named *a* and *b* but later changed to fit into the factorial system that is now being followed in the genetical studies with maize (LINDSTROM 1918).

Factor *w*, when homozygous, entirely prevents the development of normal green chlorophyll, the result being a pure white plant. Such white or albino seedlings are inherited as simple Mendelian recessives to normal green (EAST 1911, EMERSON 1912). Factor *v* (virescent), when homozygous, has the ability to repress partially or to delay the formation of green pigment. Virescent-white seedlings possess very little green color upon germinating, being almost white, but under optimum conditions of light and temperature they may develop sufficient chlorophyll to mature and set seed. In this respect they differ from the albino seedlings, which die when the food materials in the endosperm are exhausted. This furnishes an unusually distinct means of classifying the two types. When self-pollinated, the virescent-white type produces entirely virescent seedlings.

When a green plant, heterozygous for both factor pairs (*VvWw*), is self-pollinated, a 9:3:4 ratio is obtained as follows:

9 *V W*, green
3 *v W*, virescent-white
3 *V w*, white
1 *v w*, white

Sufficient data have been accumulated to establish the above interaction of factors and to show that these factors are inherited independently of each other. A summary of 9:3:4 ratios is presented in table 1.

From such a relation we can state that *w* is able to inhibit any green pigment which normally might be produced by the *V* factor or the *v* factor. Put in other words, both *V* and *W* are essential for the development of normal green chlorophyll.

TABLE 1

Summary of data showing 9:3:4 ratio derived from self-pollinated green plants heterozygous for white and virescent-white seedlings (Ww Vv).

	GREEN	VIRESCENT-WHITE	WHITE
MILES (1915)	132	36	56
LINDSTROM (1918)	640	190	268
2205– 4	44	11	26
2217–47	109	29	35
–50	102	32	54
–55	86	22	35
–58	78	23	26
–69	89	32	32
2218– 1	80	27	36
–13	54	21	36
–14	73	23	28
2219– 4	65	22	27
–28	59	29	40
2220–12	70	28	29
2670– 1	88	22	13
–11	38	19	22
–22	49	11	30
–25	28	6	11
Total.....	1884	583	804
Theoretical.....	1840	613	818

P = 0.26

Yellow and virescent-white relation (LlVv)

The next step in the analysis was the determination of the interrelation of the *Vv* and *Ll* factor pairs. Factor *l* (from *luteus*, yellow) is considered as the determiner for a distinct yellow (xanthophyll and carotin) pigment observed in certain maize seedlings (LINDSTROM 1918, plate 1).

When a green plant heterozygous for both virescent-white and yellow seedlings is self-pollinated, a 12:3:1 ratio results as follows:

9 *L V*, green
3 *l V*, green
3 *L v*, virescent-white
1 *l v*, yellow (slightly virescent)

A summary of the data to substantiate such a ratio is given in table 2.

The two types of green seedlings *LV* and *lV* have been demonstrated and thoroughly tested genetically. There is no marked phenotypic distinction between them, although there are certainly slight variations among the greens in shade of color.

This genetic hypothesis presupposes that *L* is not absolutely essential for the development of green pigment, as is *V*. What effect this dominant allelomorph *L* really produces is uncertain. A bit of indirect evidence is offered by the color of the striped leaves of the *japonica* type of maize. There are two sorts of *japonica* plants, one with green-and-white-striped leaves, the other with green-and-yellow-striped leaves (see LINDSTROM 1918, plates IV and V). It has been shown that the yellow pigment in the yellow stripes of the latter type is caused by the *l* factor, so that these

TABLE 2

Summary of data showing 12:3:1 ratios derived from self-pollinated green plants heterozygous for virescent-white and yellow seedlings (LlVv).

	GREEN	VIRESCENT-WHITE	YELLOW
Table 6 (LINDSTROM 1918)	3583	853	260
Table 8 (LINDSTROM 1918)	3058	767	256
Table 9 (LINDSTROM 1918)	676	190	54
Table 10 (LINDSTROM 1918)	608	155	65
Table 11 (LINDSTROM 1918)	380	88	33
2206–36	169	42	12
2347	637	171	56
2348	204	50	19
Total	9315	2316	755
Theoretical	9290	2322	774

P = very close fit; $\chi^2 = 0.549$

plants are factorially *jjll*. The *japonica*-white-striped plants, which possess colorless stripes, contain the *L* factor; hence, their genotypic formula is *jjLL*. In this case then, the dominant *L* factor produces no pigment whatsoever. The same might be true in the seedling types *LV* or *Lv*.

The influence of *l* in the *lV* type of green is unknown. If it produces the characteristic yellow pigment there, it would be hidden by the green. Attempts are now being made to differentiate the two types of green (*LV* and *lV*) by spectroscopic tests.

The effect of the virescent factor *v* is seen in both the *Lv* and *lv* genotypes. In the former, the virescent or greening effect is produced on white leaves; while in the latter this effect is seen on yellow leaves, so that they are really virescent-yellow seedlings.

As additional evidence of the interrelations of *L* and *V*, data from crosses between two green plants, one *LlVv* and the other *llVv* (which when self-pollinated produced 3 greens :1 yellow), and a reciprocal cross, are presented in table 3.

The close approximation to the unusual 6:1:1 theoretical ratio not only checks the factorial hypothesis but also serves to show that *L* and *V* are inherited independently of each other both in the pistillate and in the staminate mechanism for the segregation of factors.

The preceding evidence has shown that *W* and *V* are both necessary for normal green color, and that *w* can inhibit the development of any green pigment. It has also proven that *L* is not necessary for green color; and that *l* can produce yellow pigment in the presence of *v*.

What relation does *w* bear to *l*? If *w* can inhibit any green pigment produced by *v*, can it react similarly with *l*? The answer is to be found in the subsequent section.

TABLE 3

F_1 seedlings from the cross LlVv × llVv and its reciprocal.

PEDIGREE NUMBER	GREEN	VIRESCENT-WHITE	YELLOW
2343–22 × 2206–76	168	25	25
–36 × 2259–16	126	25	24
2259– 2 × 2343–22	178	27	32
Total.....	472	77	81
Theoretical (6:1:1)...	472.50	78.75	78.75

TRIHYBRID RELATIONS

P_1, F_1, F_2 and F_3 data of cross LlVvWW × LLVVWw

When the three factor pairs concerned in the development of green chlorophyll and yellow pigment are brought together by hybridization, some interesting relations become apparent. The experimental studies bearing on this situation arose from a cross of two green plants, one producing green, virescent-white, and yellow seedlings when self-pollinated, the other only green and white seedlings. Factorially this cross would be represented as *LlVv* × *VVWw*.

All the F_1 plants of this cross were completely green in the seedling and mature-plant stages. Unfortunately only 10 of the 72 green F_1 plants were self-pollinated. Their F_2 seedling progenies have been arranged in table 4.

Since one parent produces four kinds of gametes and the other only two, there should be eight different F_1 genotypes. All the eight types are not

represented among the ten progenies in table 4, which is scarcely to be expected because of the small numbers concerned. Only five of the eight appeared, namely, two kinds of greens (as shown by certain crosses); a type segregating into 3 greens to 1 white (1764–22); another into 9 greens to 3 virescent-whites to 4 whites (1764–30); and finally a new type segregating into all the four seedling types but giving a peculiar ratio of these characters. There were three seedling progenies of this latter sort (1764–4,

TABLE 4

F_2 seedling progenies from green F_1 plants of the cross LlVvWW × LLVVWw.
937–14 × 812–1.

PEDIGREE NUMBER	GREEN	VIRESCENT-WHITE	YELLOW	WHITE
1764– 4	26	4	5	4
– 5	50			
–12	58			
–16	47			
–20	59			
–22	197			61
–24	48			
–30	136	24		46
–40	59	21	15	36
–43	22	4	2	5

TABLE 5

Three F_2 seedling progenies from table 4, which produced all four types of seedlings.

PEDIGREE NUMBER	GREEN	VIRESCENT-WHITE	YELLOW	WHITE
1764– 4	26	4	5	4
–40	59	21	15	36
–43	22	4	2	5
Total.....	107	29	22	45
Theoretical (36:9:7:12)...	114	29	22	38

P = 0.64

–40, –43), and it is with them and their progeny that we shall be concerned in establishing an hypothesis to interpret the interaction of the three factors and their allelomorphs. The F_2 progenies in table 4 do not offer sufficient evidence in themselves simply because their numbers are too small, but they do agree with the hypothesis to be developed, as will be seen later.

From the three lots of the new types of seedling progenies mentioned above, which have been grouped in table 5, has come the critical evidence.

Many of the green plants from each of these three progenies (1764–4, –40, –43) were self-pollinated and the F_3 seedling progenies tested. They are arranged in table 6.

TABLE 6

Showing F_3 seedling progenies from self-pollinated green F_2 plants of table 5.

F_2 GENOTYPES	PEDIGREE NUMBER	F_3 SEEDLING TYPES				CLOSENESS OF FIT		
		Green	Virescent-white	White	Yellow	Dev. / P. E.	χ^2	P
1 *LLVVWW*	2205– 1	64						
	–16	71						
2 *LlVVWW*	2206–21	91						
	–54	100						
1 *llVVWW*	2207–10	96						
Total.....		422						
2 *LLVvWW*	2206–37	74	22					
Theoretical...		72	24			0.7		
2 *LLVVWw*	2205–10	224		56				
Theoretical...		210		70		2.9		
2 *llVvWW*	2205–11	91			31			
2 *llVVWw*	2207–12	73			24			
Total.....		164			56			
Theoretical...		165			55	0.2		
	2205–14	47			35			
	2206–23	45			29			
4 *llVvWw*	–29	70			60			
	–31	66			42			
	–75	131			78			
Total.....		359			244			
Theoretical...		339			264	2.7		
4 *LlVvWW*	2206–36	169	42		12		0.31	
Theoretical...		167	42		14			
4 *LLVvWw*	2205– 4	44	11	26				
Theoretical...		46	15	20				0.23
	2205–12	54		12	4			
4 *LlVVWw*	2206–73	150		34	11			
	–84	56		13	12			
Total.....		260		59	27			
Theoretical...		259		65	22			0.44
	2206– 2	63	18	26	15			
	–15	172	27	42	32			
8 *LlVvWw*	–46	166	28	63	31			
	–57	176	50	63	41			
	–71	78	16	21	10			
	2207–23	26	11	13	6			
Total.....		681	150	228	135			
Theoretical...		672	168	224	131			0.53

Hypothesis for factorial interactions of the three factors

From the data in tables 5 and 6 the following hypothesis has been derived. This hypothesis has four general points, namely:

1. That three pairs of factors (*Ll*, *Vv*, *Ww*) are concerned in the development of the green and yellow pigments in the maize seedlings of this experiment.
2. That these three factor-pairs undergo ordinary Mendelian segregation and recombination.
3. That they are inherited independently of each other, not linked.
4. That they exhibit certain constant interrelations.

It is only the fourth point that needs explanation. Assuming three pairs of factors with complete dominance, there are only eight possible combinations which might give different phenotypic characters, namely, *LVW*, *LVw*, *LvW*, *Lvw*, *lVW*, *lVw*, *lvW*, and *lvw*. If a green plant heterozygous for all three is self-pollinated, they would occur in the ordinary 27:9:9:3:9:3:3:1 proportion, respectively.

It will be noted that only four different phenotypes are recorded in table 5, namely green, virescent-white, yellow, and white. The distinction between these four classes of seedlings was remarkably clear. Practically all of the data were recorded before the present hypothesis was evolved, and no difficulty in classifying the material was experienced.

To account for the unusual ratio observed in the progenies of tables 5 and 6, which were segregating for the four seedling characters, the following interactions between the three pairs of factors was assumed:

27 *LVW*, green seedlings	3 *Lvw*, white seedlings
9 *lVW*, green seedlings	3 *lVw*, yellow seedlings
9 *LvW*, virescent-white seedlings	3 *lvW*, yellow seedlings
9 *LVw*, white seedlings	1 *lvw*, yellow seedling

This arrangement results in a 36:9:7:12 ratio of green : virescent-white : yellow : white. Among the F_1 genotypes of the original cross (*LlVvWW* × *LLVVWw*) there should be one of the factorial composition *LlVvWw*. According to the hypothesis this should produce a seedling progeny segregating into the 36:9:7:12 ratio. Three such progenies appear in table 5, while in the last section of table 6 there are six progenies (2206–2, –15, –46, –57, –71 and 2207–23) of the same sort. The actual data in both tables are well in accord with the hypothesis, the value for P in table 5 being 0.64 and in table 6, 0.53.

Not only are the hypothetical factor-interrelations substantiated but also the independent inheritance of the three factor-pairs is reasonably assured. However, further evidence on this appears later.

Before discussing the various functions of the individual factors, it is necessary to show that the hypothesis is verified in the F_3 generation. For this purpose the reader is again directed to table 6, which has been compiled from the data obtained by self-pollinating twenty-five of the F_2 green

TABLE 7

Showing the theoretical and actual proportions of the F_3 progenies of table 6.

F_2 GENOTYPES	F_3 SEGREGATION OF SEEDLINGS	FOUND	EXPECTED	DEVIATION
1 *LLVVWW* 2 *LlVVWW* 1 *llVVWW*	All green	5	3	+2
2 *LLVvWW*	3 green 1 virescent-white	1	1	0
2 *LLVVWw*	3 green 1 white	1	1	0
2 *llVvWW* 2 *llVVWw*	3 green 1 yellow	2	3	−1
4 *llVvWw*	9 green 7 yellow	5	3	+2
4 *LlVvWW*	12 green 3 virescent-white 1 yellow	1	3	−2
4 *LLVvWw*	9 green 3 virescent-white 4 white	1	3	−2
4 *LlVVWw*	12 green 3 white 1 yellow	3	3	0
8 *LlVvWw*	36 green 9 virescent-white 7 yellow 12 white	6	5	+1

P = 0.66

plants occurring in the 36:9:7:12 distribution listed in table 5. According to the hypothesis there should be nine different types of F_3 segregations from such F_2 plants, and they should occur in definite proportions. These types, their actual proportions, and their theoretical expectancies are arranged in table 7.

It will be noted that every one of the theoretical nine classes is represented in the F_3 generation and that the expected proportions of the classes are unusually well realized, the closeness of fit in this case being very good since P has a value of 0.66.

A glance at the individual F_3 progenies in table 6 will show that in the great majority of cases, they, themselves, conform very closely to the theoretical proportions. In no case is there any serious deviation from the demands of the hypothesis. Thus the hypothesis is fully verified by the F_3 data.

TABLE 8

Seedling progenies from self-pollinated green plants of a 9:7 ratio of green: yellow seedlings. llVvWw.

PEDIGREE NUMBER	ALL GREEN	3:1 RATIO		9:7 RATIO		Dev. / P. E.
		Green	Yellow	Green	Yellow	
2455- 1		135	60			2.7
- 6				47	48	1.8
- 7				105	93	1.3
- 8				26	19	0.4
-18				131	89	1.4
-21				96	72	0.3
-23		62	15			1.6
-27		240	93			1.8
-28				83	69	0.6
-30				106	90	0.9
2456- 4	72					
Total.....	72	437	168	594	480	
Theoretical.....	72	454	151	604	470	

Among the F_3 progenies in table 6 are several new types of ratios, notably the 9 green to 7 yellow; the 12 green to 3 white to 1 yellow; and the 36 green to 9 virescent-white to 7 yellow to 12 white. The first and third types have been analyzed, the second has not. A 9:7 ratio of green to yellow seedlings was tested further by self-pollinating eleven of the green plants in such a distribution. In table 8 the seedling progenies of these eleven plants are recorded with the view of substantiating the hypothesis.

Three kinds of progenies appear, one producing nothing but green seedlings, another giving approximately 3 green to 1 yellow, and a third repeating the 9:7 ratio of the parental stock. The proportion of the three sorts is 1:3:7 respectively.

If the hypothesis given above is correct, the 9:7 ratio of the parents was produced by a plant of the composition *llVvWw*. The 9:7 ratio would result from the following interaction of factors:

1 *llVVWW*, green	1 *llVVww*, yellow
2 *llVVWw*, green	2 *llVvww*, yellow
2 *llVvWW*, green	1 *llvvWW*, yellow
4 *llVvWw*, green	2 *llvvWw*, yellow
	1 *llvvww*, yellow

The green plants should produce three kinds of progenies in the ratio of 1:4:4. The actual proportion of 1:3:7 is fairly well in accord with this, and the individual progenies of table 8 are reasonably close to expectation, thus providing another check on the factorial hypothesis.

Another very interesting and critical bit of evidence on the factorial interrelations of the seedling chlorophyll-factors was afforded by a detailed study of the yellow seedlings. It was noted that these were actually of two types. One was strikingly pure yellow in color while the other had slight traces of green pigment, especially at the ligule and leaf tips, but not enough to hide the yellow pigment. The two types were not differentiated until most of the material used in these experiments had been grown and destroyed, hence all the yellows are classed together in the preceding tables.

TABLE 9

Classification of yellow seedlings according to presence and absence of virescent pigment.

PEDIGREE NUMBER	PURE YELLOW *lVw* AND *lvw*	VIRESCENT-YELLOW *lvW*
2455– 6	5	4
–18	20	15
2205–14	12	13
2206–15	11	12
–23	10	9
–29	25	21
–31	16	17
–46	10	8
–57	20	17
–71	4	3
–75	26	14
2207–23	4	2
Total	163	135
Theoretical (4:3)	170	128

Later plantings of some of the remaining seed were made, however, and the pure yellows were classified separately from those with traces of green. These data are placed in table 9. The pedigree numbers therein can be traced directly to tables 6 and 8.

A total of twelve progenies which possessed yellow seedlings shows that there are slightly more of the pure yellow type than of the green-yellow or virescent-yellow. In fact they occur in almost a 4:3 ratio, respectively. The explanation of this proportion is as follows.

Factorially there are three, and only three, types of yellow seedlings; *lVw*, *lvw* and *lvW*; and in an F_2 generation they should occur in a ratio of 3:1:3 respectively. All three types develop yellow pigment because of the *l* factor. The types *lVw* and *lvw* possess no green pigment since *w* inhibits any green color produced by either *V* or *v*. Hence, these two types are pure yellow. The third type *lvW* possesses the *v* factor which permits a partial development of green pigment (virescent), and since *w* is not present this virescent or green pigment is not inhibited. Therefore this third type is really a virescent-yellow seedling, differing from the virescent-white type in that the latter shows the virescent or partial green pigment on whitish leaves, the former on yellow leaves.

The 3:1:3 ratio noted above can then be grouped into a 4:3 proportion of pure yellow to virescent-yellow seedlings. The data in table 9 agree with such an interpretation reasonably well, the deviation being only 1.2 times the probable error.

With such checks as these, the F_2 and F_3 data offer beyond any reasonable doubt a satisfactory confirmation of the hypothesis to account for the inheritance of the green and yellow pigments in maize seedlings. It must not be inferred, however, that the *L*, *V*, and *W* factors are the only ones to be found. Presumably they are only some of the more fundamental ones. The writer has discovered two others in material from other sources but their interrelations with *L*, *V* and *W* are not as yet determined.

GROUP RELATIONS OF THE SEEDLING FACTORS

Independence of L, V and W proven by F_2 and F_3 data

Previous experiments have shown that *W* and *V* are not linked. The same is true of the *L* and *V* factors. This leaves only the *L* and *W* relation open. The trihybrid data in this article afford critical evidence on the independent inheritance of *L* and *W* as well as of the others. Since backcrosses cannot be obtained in these seedling studies, one must rely on F_2 and F_3 data to determine the group relations of the factors involved.

Combining the F_2 and F_3 data (tables 5 and 6) which show the trihybrid relationship (*LlVvWw*), we obtain the following totals:

Observed, 788 green: 179 virescent-white: 157 yellow: 273 white.

Calculated, 786 green: 196 virescent-white: 153 yellow: 262 white.

When the closeness of fit, based on independent inheritance of all three factor-pairs, is determined, the value for P becomes 0.56. Hence theory and fact agree sufficiently well to justify the hypothesis of independent inheritance between *L*, *V* and *W*.

Independence of L, V and W proven by relation to the R aleurone-factor

The fact that *L*, *V* and *W* are located in different groups or on separate chromosomes is also checked by the relations of these factors to the *R* factor concerned in aleurone-color development in the maize kernel.

Data have been published (LINDSTROM 1920) to show that *W* and *R* are inherited independently of each other. Three F_2 seedling progenies from self-pollinated green F_1 plants of the composition *AACCRrWw* have produced the following relation:

	RW	*Rw*	*rW*	*rw*
Observed	482	155	180	52
Calculated	489	163	163	54

The deviations from a 9:3:3:1 ratio of independent inheritance between *R* and *W* are not marked. In fact when the closeness of fit is determined, P has a value of 0.51 showing that the deviations can very well be accounted for by errors of random sampling. Hence, *W* and *R* are not linked but are located on separate chromosomes.

The independent inheritance of *R* and *V* is also established by a large F_2 population which was derived from self-pollinating thirty-four F_1 plants of the composition *AACCRrVv*. A total of these 34 progenies is recorded as:

	RV	*Rv*	*rV*	*rv*
Observed	2080	730	716	221
Calculated	2108	702	702	234

In this case the deviations from a 9:3:3:1 ratio are not wide enough to vitiate the hypothesis of independent inheritance of *R* and *V*. The value for P is 0.48 in this distribution.

Linkage of R and L factors

From such data we are justified in assuming that *W*, *V* and *R* are located on separate chromosomes. In a previous publication (LINDSTROM 1918) evidence was presented to show that the *L* factor was linked with a certain aleurone factor, which at that time had not been definitely isolated. Since then the material has been tested with appropriate aleurone testers of known constitution obtained from Dr. R. A. EMERSON of CORNELL UNIVERSITY, and it has been definitely determined that it is the *R* factor which

TABLE 10

Seedling progenies from self-pollinated green plants of the composition RLv.rlV(WWAACCP$_r$P$_r$).

PEDIGREE NUMBER	FROM COLORED-ALEURONE SEED			FROM COLORLESS-ALEURONE SEED		
	Green	Virescent-white	Yellow	Green	Virescent-white	Yellow
2343– 7	42	0	0	0	0	0
–15	41	0	0	0	0	0
–62	38	0	0	0	0	0
– 1	28	0	0	20	0	0
–13	27	0	0	22	0	0
–26	28	0	0	13	0	0
–40	28	0	0	24	0	0
–41	18	0	0	19	0	0
–18	129	50	0	0	0	0
–21	103	42	0	0	0	0
–23	141	46	0	0	0	0
–47	26	8	0	0	0	0
– 6	121	27	0	53	0	17
–10	156	50	1	59	1	22
–14	42	12	0	26	1	10
–19	157	53	0	60	1	19
–24	186	52	1	60	1	18
–25	67	23	0	22	1	10
–30	229	75	0	72	0	27
–31	179	50	0	66	1	25
–33	142	51	0	59	3	11
–36	150	51	0	68	3	13
–43	159	57	0	48	0	19
–45	118	41	0	64	11	16
2344– 1	0	0	0	37	0	0
– 6	0	0	0	30	0	0
– 9	0	0	0	34	0	0
–12	0	0	0	29	0	0
–19	0	0	0	33	0	0
–20	0	0	0	31	0	0
–21	0	0	0	30	0	0
– 3	0	0	0	92	0	28
– 5	0	0	0	75	0	30
– 8	0	0	0	110	0	35
–11	0	0	0	53	0	18
–13	0	0	0	104	0	23
–14	0	0	0	97	0	19
–17	0	0	0	93	0	27
–18	0	0	0	74	0	37
–23	0	0	0	81	0	22

is linked with *L*. Additional evidence on this situation will be presented here.

Since back-crosses cannot be used to test the linkage (because the double recessive is not viable), the F_2 and F_3 generations must suffice. By self-pollinating a large number of plants of the factorial composition *RLv.rlV* (*WWAACC*), it has been possible to demonstrate that *R* and *L* are very closely linked with each other. The results of such self-pollinations are arranged in table 10.

Since only the *Rr* factor-pair for aleurone color is heterozygous in this material, colored-aleurone grains show that the plants developing from them possess the *R* factor, while those plants coming from colorless-aleurone seed possess only the *r* factor. A glance at table 10 shows that among the 24 ears from colored seed (2343), there were 7 that bred true for colored aleurone, while 17 ears showed a segregation into colored and colorless grains (all 3:1 ratios in this material). The expectation here would be 8 and 16 respectively. The progenies from colorless grains bred true for colorless aleurone (2344).

TABLE 11

Summary of seedling progenies of table 10 showing behavior of seedling factors, LIVv.

	ALL GREEN	12 GREEN: 3 VIRESCENT-WHITE: 1 YELLOW	3 GREEN: 1 VIRESCENT-WHITE	3 GREEN: 1 YELLOW
	4 {1 *LLVV* 2 *LlVV* 1 *llVV*	4 *LlVv*	2 *LLVv*	2 *llVv*
Found	15	12	4	9
Expected (4:4:2:2)	13.3	13.3	6.7	6.7
Deviation	+1.7	−1.3	−2.7	+2.3

P = 0.53

As regards the behavior of the seedling-chlorophyll factors themselves, their inheritance obeys the demands of the hypothesis, as can well be seen in the summary that has been arranged in table 11.

With the data agreeing so well in respect to the aleurone and chlorophyll factors separately, we can turn directly to the interrelation between them. It will be noted that in table 10, among those progenies segregating for seedling characters, the normal 12:3:1 ratio does not obtain if one considers those progenies coming from colored seed separately from those developing from colorless grains. In other words very few (only two in this case) yellow seedlings come from colored seed, and only a few virescent-whites appear in the progenies from colorless seed. This means that when-

ever *R* is present, *l* is not likely to be, whereas if *r* is present *L* is rarely found. Stated in terms of linkage, the parental combinations *RL* and *rl* exhibit very close linkage; the crossover classes *Rl* and *rL* are correspondingly rare.

The raw data in table 10 are not adapted for a quantitative determination of the percentage of crossing over between *R* and *L*. The material in this experiment was segregating for a pericarp color as well as for aleurone color and chlorophyll factors. This pericarp color prevents an accurate classification of aleurone color, a correct classification of which is absolutely essential in determining the presence of the crossover classes. There were certain ears, however, with colorless pericarp which permitted an accurate separation into colored and colorless aleurone. The data from these ears have been gathered into table 12.

TABLE 12

Summary of seedling progenies of table 10 from ears which possessed colorless pericarp.

PEDIGREE NUMBER	FROM COLORED ALEURONE			FROM COLORLESS ALEURONE		
	Green	Virescent-white	Yellow	Green	Virescent-white	Yellow
2343–10	156	50	1	59	1	22
–19	157	53	0	60	1	19
–24	186	52	1	60	1	18
–25	67	23	0	22	1	10
–30	229	75	0	72	0	27
–31	179	50	0	66	1	25
Total	974	303	2	339	5	121
Theoretical (independent inheritance)	959	240	80	349	87	29

If the factors *R* and *L* were independently inherited we should expect a 12:3:1 ratio of green to virescent-white to yellow seedlings from both colored and colorless seed in table 12, whereas from the colored aleurone only 2 yellow seedlings actually occurred where 80 would be expected, and from colorless aleurone only 5 virescent-whites appeared where the expectation would be 87. Evidently then the parental gametes *RL* and *rl* are produced far in excess of the crossover gametes *rL* and *Rl*. In fact, the latter are produced so infrequently that the relationship approaches complete linkage.

The appearance of the crossover classes was very distinct, however, and in each case the aleurone color of the seed producing the crossover seedling was checked by digging up the plant and examining the grain for its aleurone color. Their chlorophyll type was unmistakable as was their aleurone

appearance, although the latter offers a slight source of uncertainty since experience has shown that very rarely a seed which is apparently colorless will produce colored progeny, indicating that it possessed the requisite factors although something acted to prevent their full expression in the mother seed. This would explain a very infrequent occurrence of a virescent-white from apparently colorless seed but would not account for the occurrence of yellow seedlings from colored seeds. Unfortunately it was impossible to mature these seedlings and actually test them. Inasmuch as the aleurone classification was made in an exceedingly careful manner, and the seeds planted so as to prevent accidental mixing, it seems reasonable to suppose that we are dealing with actual crossover types, and that *R* and *L* are not completely linked.

As to the quantitative measure of linkage between *R* and *L*, this can best be determined by taking from table 12 only the data in which *R* and *L* are directly concerned. The green classes are eliminated from consideration since both *L* and *l* (*LV* and *lV*) are grouped there. Using then only the critical data, the following distribution obtains:

RLv	*Rlv*	*rLv*	*rlv*
303	2	5	121

If there were independent inheritance between *R* and *L*, this distribution should resemble a 9:3:3:1 ratio. Obviously the departure therefrom is abnormally great. Instead of a 1:1 gametic ratio, a 60:1 ratio fits the data better, the theoretical expectation being 317:4:4:106 in this case. That is, the non-crossover classes are produced sixty times more often than the crossover classes. The percentage of crossing over between *R* and *L* consequently, is about 1.6 percent in this experiment. The numbers upon which this percentage is based are, however, rather small, especially since they are F_2 data; hence, the crossover percentage of 1.6 percent is presumably more or less inaccurate.

The occurrence of the crossover classes *Rl* and *rL*, although they have not been proven by tests other than phenotypic appearance, indicates that the factors *R* and *L* are not identical, as might have been supposed from preliminary studies reported earlier (LINDSTROM 1918) where the limited data pointed only to complete linkage. In this connection it might be noted that the factors *Rr* and *Gg* (the latter factor-pair of which the homozygous recessive condition *gg* produces a golden plant) have been found to show 23 percent crossing over, while *Ll* and *Gg* show 19 percent crossing over. If *R* and *L* are not identical but show a crossover percentage of 1.6 percent then the order of the factors must be *R-L-G*, and the difference between 23 percent and 19 percent might possess some significance, although these crossover percentages also are based on relatively small numbers.

DISCUSSION

During the six years which have elapsed since these genetical investigations on chlorophyll in maize seedlings were begun, the inheritance of the three types of abnormal seedlings, white, virescent-white and yellow, has proven itself to be typically Mendelian. The stability of the types has been such that no practical difficulty in classifying them from year to year has arisen, especially when they were grown under optimum conditions. It is true that only the most clearly defined types were chosen to carry on the investigations. This was done to remove any possible modifying factors which would have a tendency to obscure the fundamental relations between the basic factors. That there are such modifying factors is certain. But their influence is to be studied only after the fundamental factors have been isolated and tested genetically. Such a procedure is entirely natural and justifiable if we can prove that these fundamental factors, when so isolated, behave as relatively stable units and follow some definite system of inheritance. This is the true situation with respect to the seedling types of maize. The fundamental factors *Ww*, *Vv* and *Ll* are expressed as stable seedling characters which exhibit strict and typical Mendelian inheritance.

The genetic analysis of the three factors, *w*, *v* and *l*, the first two of which are related to the development of green pigment and the third to the formation of yellow color, has established a definite interrelation between these factors that should offer some suggestions as to their chemical or physiological behavior. Whether one can draw an analogy between genetic relations and chemical or physiological relations is still in the realm of speculation. It seems reasonable to suppose however, that the two processes are not independent, and that future development will see them intimately related with each other.

Our genetic hypothesis has demonstrated that the various types of maize seedlings possess the following factors:

Green	*LVW* and *lVW*
Virescent-white	*LvW*
White	*LVw* and *Lvw*
Virescent-yellow	*lvW*
Pure yellow	*lVw* and *lvw*

From this series of interrelations we can derive several interesting and critical suggestions as to the relationship between the green and yellow pigments here concerned.

For the complete development of green color it seems that there are at least two factors necessary, *W* and *V*. It must not be thought, however,

that these two are the only ones concerned. Suggestions are now at hand of another factor which apparently interacts with *W* to give a 9:7 ratio of green to white seedlings. Green pigment is then dependent on two, possibly three factors. How are these green-producing factors and their allelomorphs related to yellow pigment?

A genetic relationship between green and yellow pigment, as shown by the factorial behavior, is clearly seen in the action of the *w* factor. This factor is able to inhibit or repress the green or virescent color produced by *v* but does not interfere with the development of the yellow pigment produced by *l*.

This is most definitely seen by considering the four genotypes, *LVw*, *Lvw*, *lVw*, and *lvw*, of which the first two are white and the last two yellow. In the first type (*LVw*), *w* inhibits any green pigment which might be produced by *V* or even *L;* and in the second genotype (*Lvw*) it even represses the slight amount of green pigment caused by *v* as well as any pigment that might be produced by *L*. In the third type (*lVw*), however, although *w* inhibits any green-producing effect of the *V* factor, it does permit the yellow pigment caused by *l* to appear, producing a pure yellow seedling. If *w* were replaced by *W* in this type, the result would be a green seedling (*lVW*) in which the yellow pigment caused by *l* would presumably be hidden by the green color. The fourth genotype (*lvw*) is also pure yellow because *w* prevents the virescent or greening effect of *v* from functioning but allows *l* to form its yellow pigment. These reactions of the *w* factor can be resolved into the simple statement that a plant possessing the *w* factor lacks something essential for the development of normal green pigment but not for the development of yellow pigment, which apparently is normally produced whenever *l* is present.

Genetically, then, green and yellow pigment in this respect are independent of each other. Whether such independence of action actually occurs between the formation of the chlorophyll and xanthophyll pigments in leaf tissue is at present unknown. It is entirely possible that the formation of these two pigments is unrelated, at least in some stage of development, and this genetic relation offers some such suggestion.

The fact that all three factor-pairs concerned in the formation of green and yellow pigment are located in different groups or in different chromosomes agrees with the situation in Drosophila, namely, that factors which are closely related as to their phenotypic expression are not necessarily grouped together in the germ-plasm. This of course is also true for aleurone color in maize, for which three factors (*A*, *C*, *R*) are responsible, all of them being located in different chromosomes.

SUMMARY

1. The inheritance of three factors, *w* (white), *v* (virescent) and *l* (yellow), and their respective allelomorphs, *W*, *V* and *L*, which govern the formation of green and yellow pigments in maize seedlings, is shown to be typically Mendelian.

2. A summary of previous work, including some new data, showing the interaction between the factors *Ww* and *Vv* and between *Vv* and *Ll* is given.

3. An hypothesis to explain the trihybrid interaction of the factors is proposed. The F_2 generation of the trihybrid *LlVvWw*, based on this hypothesis, results in a 36:9:7:12 ratio of green : virescent-white : yellow : white seedlings, respectively, with which the actual data are well in accord.

4. The F_2 and F_3 data show that the factors *L*, *V* and *W* are inherited independently of each other.

5. The factors *W* and *V*, which are necessary for the formation of green pigment, show no interaction with *l* which is concerned in the formation of the yellow pigment in seedlings. Factor *w* interacts with *v* but not with *l*. In other words, *w* inhibits the virescent-green pigment produced by *v* but allows the yellow pigment produced by *l* to develop independently.

6. The independent inheritance of *Ll*, *Vv* and *Ww* is also shown by their relations to the *Rr* factor-pair for aleurone-color development, both *Ww* and *Vv* being inherited independently of *Rr*.

7. Very close linkage between *Rr* and *Ll* is demonstrated. Crossing over occurs very infrequently.

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